

A revision of *Danielssenia* Boeck and *Psammis* Sars with the establishment of two new genera *Archisenia* and *Bathypsammis* (Harpacticoida: Paranannopidae)

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SYNOPSIS. *Archisenia* gen. nov. is proposed to accommodate the *sibirica*-group of the genus *Danielssenia* Boeck, 1872. Re-examination of Alaskan material of *D. stefanssoni* Willey, 1920 has shown the latter species to be a junior synonym of *D. sibirica* Sars, 1898, the type and only species of the new genus.

Danielssenia robusta Sars, 1921 and *Fladenia intermedia* (Wells, 1965) are synonymous and consequently *F. robusta* comb. nov. becomes the type species of the genus *Fladenia* Gee & Huys, 1990. *Danielssenia similis* Chislenko, 1971 is regarded as *species inquirenda* and the genus *Danielssenia* is redefined from the type species *D. typica* Boeck, 1872, and two other species (*D. quadriseta* Gee, 1988 and *D. reducta* Gee, 1988).

The status of *D. fusiformis* (Brady, 1880) nec Sars (1910) is reconsidered and as a result the genus *Sentirenia* Huys & Gee, 1992 is relegated to a junior synonym of *Jonesiella* Brady, 1880 which is reinstated to accommodate *J. fusiformis* Brady, 1880 and *J. eastwardae* (Coull, 1971) comb. nov.

Psammis borealis Klie, 1939 is removed from the genus *Psammis* Sars, 1910 but retained in the Paranannopidae as *species incertae sedis*. *P. longifurca* Bodin, 1968 is transferred from *Psammis* to *Bathypsammis* gen. nov. The genus *Psammis* is redefined on the basis of the type species *P. longisetosa* Sars, 1910, and *P. longipes* Becker, 1974.

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A detailed redescription of *A. sibirica* and new illustrations of *D. typica*, *P. longisetosa*, *P. longipes* and *B. longifurca* are provided.

Intersexuality in copepods and the possible phylogenetic relationships of *Danielssenia*, *Psammis*, *Fladenia*, *Archisenia* gen. nov. and *Bathypsammis* gen. nov. are briefly discussed.

A key to the genera of the Paranannopidae is presented.

INTRODUCTION

Throughout its taxonomic history up to the late 1980s, the genus *Danielssenia* Boeck, 1872 has served as a repository to accommodate different kinds of 'tachidiid' harpacticoid copepods, in so far that the distinction between this genus and *Psammis* Sars, 1910 almost became no longer tenable (Wells, 1965, 1967). Gee (1988a) pointed out that differences in mandibular gnathobase structure, possibly reflecting different diets, could indicate that both genera are trophically isolated, but admitted that perhaps more solid morphological evidence is necessary to maintain generic distinction.

The criteria applied by most workers to allocate newly discovered species to *Danielssenia* generally had no phylogenetic significance as they were mainly based on plesiomorphic character states (i.e. P1 not modified) which are diagnostic of a wider group of families. Virtually no effort has been made to correctly assess the sexual dimorphism on the swimming legs and very little information on detailed mouthpart structure has been documented. Both categories of characters have nevertheless proved to hold a high phylogenetic information content that can be used to determine relationships within the *Danielssenia*-*Psammis* core group of genera (Gee & Huys, 1990, 1991; Huys & Gee, 1992, in press).

The impact of Lang's (1944, 1948) classification of the Tachidiidae also caused people to lose sight of the relationships of this core group with taxa beyond the family boundaries. The fact that his artificial subdivision into three subfamilies constrained the development of alternative phylogenetic scenarios for a long time is illustrated by the ongoing discovery and description of numerous new species of *Paranannopus* Lang, 1936 (placed in the Cletodidae and subsequently in the Paranannopidae) and *Danielssenia*

(placed in the Thompsonulinae, Tachidiidae) in the post-Langian era without any recognition of the close relationship between these two taxa. Huys & Gee (1990) inevitably had to break down the concept of the Thompsonulinae before they could re-allocate the 'danielsseniid genera' to the Paranannopidae. This group of genera essentially represents the continental shelf lineage of the family with a few species that secondarily explored deeper habitats (e.g. *Leptotachidia iberica* Becker, 1974). Its affinity to the predominantly deepwater group, containing *Paranannopus* and *Cylindronannopus* Coull, 1973, has recently been supported by the redescription of *Fladenia* Gee & Huys, 1990, a possible 'missing link' between both lineages (Gee & Huys, 1990).

This paper is the final contribution to a revision of the genus *Danielssenia*, including the allocation of the *sibirica*-group to a new genus *Archisenia*, thus reducing the number of species previously referred to the genus from 14 to four (Table 1). It also presents a revision of the other major genus *Psammis*, resulting in the proposal of a new genus *Bathypsammis*. With the revision of these taxa the establishment of novel genera draws to a close and, accordingly, a key to genera of the Paranannopidae is presented.

MATERIALS AND METHODS

Before dissection, the habitus was drawn and body length measurements were made from whole specimens temporarily mounted in lactophenol. Specimens were then dissected in lactic acid, the parts mounted in lactophenol and the preparations sealed with glyceel® (BDH Chemicals Ltd, Poole, England). All drawings of the specimens were prepared using a camera lucida on a Leitz Dialux 20 or Leitz Diaplan

Table 1 Re-allocation of species previously referred to *Danielssenia* Boeck, 1872.

Species previously referred to <i>Danielssenia</i>	Current status	Reference
<i>typica</i> Boeck, 1872	<i>Danielssenia typica</i> Boeck, 1872	Gee (1988)
<i>fusiformis sensu</i> (Sars, 1910)	<i>Danielssenia typica</i> Boeck, 1872	Gee (1988), present account
<i>quadrisseta</i> Gee, 1988	<i>Danielssenia quadrisseta</i> Gee, 1988	Gee (1988)
<i>reducta</i> Gee, 1988	<i>Danielssenia reducta</i> Gee, 1988	Gee (1988)
<i>similis</i> Chislenko, 1978	<i>Danielssenia similis</i> Chislenko, 1978 [<i>sp. inq.</i>]	present account
<i>sibirica</i> Sars, 1898	<i>Archisenia sibirica</i> (Sars, 1898) comb. nov.	present account
<i>stefanssoni</i> Willey, 1920	<i>Archisenia sibirica</i> (Sars, 1898) comb. nov.	present account
<i>fusiformis</i> Brady, 1880	<i>Jonesiella fusiformis</i> Brady, 1880	present account
<i>perezi</i> Monard, 1935	<i>Jonesiella fusiformis</i> Brady, 1880	present account
<i>paraperezi</i> Soyer, 1970	<i>Jonesiella fusiformis</i> Brady, 1880	Huys & Gee (1992), present account
<i>eastwardae</i> Coull, 1971	<i>Jonesiella eastwardae</i> (Coull, 1971) comb. nov.	Huys & Gee (1992), present account
<i>robusta</i> Sars, 1921	<i>Fladenia robusta</i> (Sars, 1921) comb. nov.	present account
<i>intermedia</i> Wells, 1965	<i>Fladenia robusta</i> (Sars, 1921) comb. nov.	Gee & Huys (1988), present account
<i>spinipes</i> Wells, 1967	<i>Afrosenia spinipes</i> (Wells, 1967)	Huys & Gee (in press)
<i>minuta</i> Coull, 1969	<i>Sentropsis minuta</i> (Coull, 1969)	Huys & Gee (in press)

differential interference contrast microscope. The terminology for body and appendage morphology is according to Huys and Boxshall (1991). Abbreviations used in the text and figures are P1–P6 for thoracopods 1–6; exp(enp)-1 (-2,-3) to denote the proximal (middle, distal) segment of a ramus. Body length was measured from the base of the rostrum to the posterior margin of the anal somite.

SYSTEMATICS

Family Paranannopidae Por, 1984

Genus *Archisenia* gen. nov.

SYNONYMY. *Danielssenia* Boeck, 1872 (part).

DIAGNOSIS. Paranannopidae. Body large, slightly fusiform and dorso-ventrally flattened. Rostrum not hyaline, with 2 pairs of small sensillae. Somatic hyaline frills minutely dentate. Female genital double-somite with lateral and ventral sub-cuticular ridge marking original segmentation; genital field with minute copulatory pore and sinusoidal copulatory duct leading to transverse seminal receptacle partly located anterior to genital slit; P6 with 1 outer plumose seta and 2 minute spiniform elements. Pseudoperculum hyaline with dentate margin. Caudal rami slightly divergent and slightly longer than broad. Female antennule 6-segmented; aesthetasc on segment 4; distal 2 segments with heavily pectinate spines. Antennary exopod 3-segmented with armature formula [2-1-3]. Mandibular coxa elongate, with blunt teeth on gnathobase; basis with 4 setae; endopod 1-segmented; exopod 2-segmented. Maxilliped subchelate with 1 large and 1 small seta on syncoxa; basis with naked seta on palmar margin, endopodal claw with 2 accessory setae. P1 exopod 3-segmented, exp-3 with distal outer spine longer than middle outer spine; endopod longer than exopod, 2-segmented, enp-2 4.5 times longer than broad, inner seta implanted medially. P2–P4 intercoxal sclerites with spinules or setules on distal margin; rami 3-segmented; exp-1 with inner seta; female P2–P3 enp-2 with small apophysis at outer distal corner. Armature formula of P1–P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.223	1.1.221
P3	1.1.323	1.1.321
P4	1.1.323	1.1.221

Female fifth pair of legs not fused medially; exopod and baseoendopod separate, each with 5 setae, inner seta on exopod well separated from remaining 4 setae.

Male with sexual dimorphism on antennule, P1, P2 endopod, P3 endopod, P5, P6 and in genital segmentation. Antennule 9-segmented, subchirocer; segment 6 very swollen, with aesthetasc. P1 inner basal spine less strongly developed, segments of rami more slender and spinule rows on outer margin of endopod much smaller. P2 enp-1 larger, with inner seta transformed into a non-articulating process; enp-2 without inner seta, outer distal corner attenuated into a long apophysis reaching far beyond the distal border of enp-3;

enp-3 with distal outer spine partially fused to segment, much shorter and stronger than in female, with spinules reduced to coarse teeth, other setae reduced in size. P3 enp-2 with inner distal corner slightly attenuated, outer distal corner attenuated into a hook-shaped apophysis. Fifth pair of legs fused medially; baseoendopod and exopod separate with 2 and 5 setae, respectively. P6 symmetrical, fused to somite, with 3 setae each.

TYPE SPECIES. As a result of the arguments and analysis put forward below we regard *D. stefanssoni* Willey, 1920 as a junior synonym of *D. sibirica* Sars, 1898 and therefore *A. sibirica* (Sars, 1898) comb. nov. is designated as the type species.

OTHER SPECIES. None.

ETYMOLOGY. The generic name is derived from the Greek prefix *archi*, meaning first in time and alludes to the primitive position in the family. Gender: feminine.

Archisenia sibirica (Sars, 1898) comb. nov.

SYNONYMY. *Danielssenia sibirica* Sars, 1898; *Danielssenia stefanssoni* Willey, 1920.

MATERIAL EXAMINED.

— National Museum of Natural History (Smithsonian Institution), Washington, D.C.: 8 ♀♀ and 1 ♂ from Point Barrow, Nuwuk Lake, Alaska, U.S.A.; collected by R. Lewis *et al.*, August 1 1960, bottom sample A974; identified as *D. stefanssoni* by M.S. Wilson; 1 ♀ dissected on 13 slides, 1 ♂ dissected on 7 slides, others preserved in alcohol: reg. no. USNM 204769.

— Naturhistoriska Riksmuseet, Stockholm: 1 ♀ and 1 ♂ from East Greenland, Barclay Bay; collected by Jespersen, July 14 1932; identified as *D. stefanssoni* by K. Lang; preserved in alcohol; reg. no. Cop. 31.

DESCRIPTION OF FEMALE. Body slightly dorso-ventrally flattened (as for male, Fig. 9B); length 0.97–1.242 mm (\bar{x} = 1.15 mm; n = 7); urosome clearly demarcated from prosome. Cephalothorax rounded anteriorly, widest near posterior margin. Rostrum (Fig. 2A) not hyaline; tapering anteriorly; with 2 pairs of sensillae. Free prosomites each with a dorsal row of spinules and some sensillae near posterior margin; hyaline frill of prosomites minutely dentate. All urosomites (Fig. 1A–B) with lateral row of spinules; first to third urosomites with dorsal row of spinules, 2 rows dorsally on genital somite; ventral spinule row on posterior border of genital double-somite and succeeding urosomites, slightly anterior to lateral rows. Genital double-somite (Fig. 1A–B) with lateral and ventral subcuticular ridge. Genital field (Fig. 1C–D) with minute copulatory pore posterior to genital slit; copulatory duct sinusoidal (Fig. 1D) leading to single, transversely elongate seminal receptacle located at level of genital slit; vestigial P6 with 1 plumose seta and 2 spinules (vestigial setae?); paired, blind ending, cuticular invaginations posterior to genital field (Fig. 1C). Hyaline frill of urosomites minutely dentate, that of penultimate somite extended to form pseudoperculum (Figs. 1B, 8C). Anal somite deeply incised. Caudal rami (Figs. 1E, 5F, 8C) tapering posteriorly, slightly longer than broad, with short spinule row medially on lateral margin and a latero-ventral spinule row on distal margin which also has a large pore near ventral outer corner (Fig. 1E); seta I minute (Fig. 5F); setae IV & V well

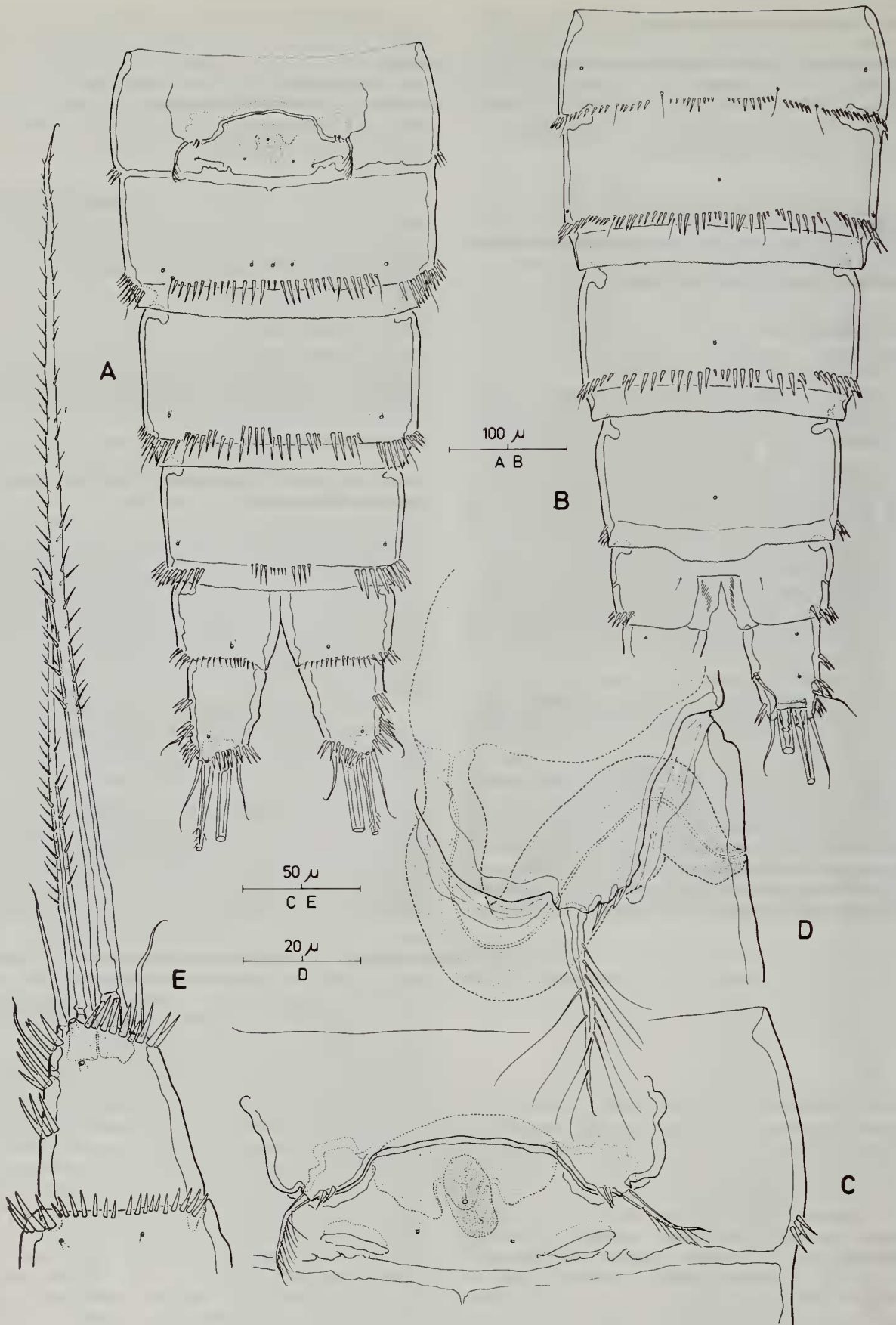


Fig. 1 *Archisenia sibirica* comb. nov. A, Female urosome (excluding P5-bearing somite), ventral view; B, same, dorsal view; C, female genital field, ventral view; D, same lateral view; E, caudal ramus, ventral view.

developed, spinulose in distal portion (Fig. 1E); seta VII tri-articulate (Fig. 8C).

Antennule (Fig. 2A–B) 6-segmented; segment 1 with 2 spinule rows on outer margin and a plumose seta at outer distal corner. Segment 2 with 5 pinnate and 1 naked setae on outer margin and 2 pinnate and 1 naked setae posteriorly directed on dorsal margin. Segment 3 with 2 pinnate and 6 naked setae at outer distal corner. Segment 4 with 6 naked setae and an aesthetasc. Segment 5 with 3 pectinate spines, 3 naked and 2 pinnate setae. Segment 6 with 1 pectinate spine and 7 naked setae.

Antenna (Fig. 2C–D). Coxa with a row of spinules proximally. Allobasis with long spinules at base of abexopodal, pinnate seta. Exopod 3-segmented with armature formula [2-1-3]; distal segment elongate with subterminal row of spinules. Endopod with 2 spinule rows on outer margin; 2 spines, a geniculate seta and a naked seta subdistally (Fig. 2C); distal margin with a pectinate spine, 4 geniculate setae, a small plumose seta (Fig. 2C) and a very small naked seta (Fig. 2D).

Mandible (Fig. 3A–B). Coxa (Fig. 3B) elongate, slender, with 2 median rows of spinules; gnathobase with bidentate and unidentate teeth and a pinnate seta at inner distal corner. Palp biramous. Basis (Fig. 3A) with patch of spinules medially and 4 pinnate setae on distal margin. Exopod 2-segmented; proximal segment with 2 pinnate setae laterally and a row of large spinules distally; distal segment with 3 apical setae. Endopod 1-segmented with 3 lateral and 6 distal setae.

Labrum (Fig. 3C) with numerous spinule rows near median distal margin of posterior face.

Maxillule (Fig. 3D). Praecoxal arthrite with 2 juxtaposed setae medially on anterior surface and 9 bidentate or pinnate spines and 1 naked seta on distal margin. Coxal endite with 5 armature elements on distal margin. Basal endite with 2 subdistal setae and 4 setae on distal margin. Rami 1-segmented and each with 3 setae.

Maxilla (Fig. 4B). Syncoxa with spinule row at outer proximal corner and with 3 endites each with 1 fused and 2 articulating pinnate spines. Allobasal endite with a fused pinnate claw, a pinnate spine and 2 setae. Endopod 1-segmented with a pinnate spine and 3 setae.

Paragnaths (Fig. 4A) well developed; with several rows of fine spinules laterally and medially; anterior face with coarse teeth.

Maxilliped (Fig. 4C). Syncoxa with numerous spinule rows, 1 large subterminal and 1 smaller terminal pinnate seta. Basis with row of spinules and a naked seta on palmar margin. Endopodal claw as long as basis, spinulose distally and with 2 accessory setae proximally.

P1 (Fig. 5A). Intercostal sclerite rectangular with 2 groups of setules on each side. Coxa with rows of spinules on anterior face and outer margin. Basis with row of spinules on inner and distal margin and around base of inner pectinate spine (Fig. 1D) and outer pinnate seta. Exopod 3-segmented, each with row of spinules on outer margin, outer spines pectinate, distal outer spine on exp-3 longer than middle outer spine. Endopod longer than exopod, 2-segmented; proximal segment slightly longer than broad, distal segment about 4.5 times longer than broad, inner seta implanted medially.

P2–P4 (Figs. 6A, 7A, 8A). Intercostal sclerite with row of spinules or setules on each side. Both rami 3-segmented, equal in length in P2 but with endopod shorter than exopod in

P3 and P4; all segments with rows of spinules on outer margin; P2 and P3 with a large spinule at base of each inner seta on enp-2 and -3. Exp-1 with inner seta; enp-2 with outer distal margin somewhat attenuated. Armature formula of swimming legs as in generic diagnosis.

Fifth pair of legs (Fig. 11D) not fused medially; exopod and baseoendopod separate. Baseoendopod with short row of spinules at base of exopod and setophore of outer seta; endopodal lobe well developed, tapering distally, with 5 pinnate setae, second outer seta longest. Exopod wider than long, boundary with baseoendopod straight, not reaching to distal margin of endopodal lobe; with 5 pinnate setae, 4 grouped together on distal outer margin and 1 well separated near inner distal corner.

DESCRIPTION OF MALE. As in female except for following characters.

Body (Fig. 9). Length 1.008 mm ($n = 1$); second and third urosomites not fused and ornamental spinules on urosome somewhat more robust (Fig. 11A).

Antennule (Fig. 10) 9-segmented, subchirocer with 6th segment very swollen, geniculation between 6th and 7th segments. Segmental fusion pattern: I, II, III–VIII, IX–XII, XIII, XIV–XX, XXI–XXIII, XXIV–XXV, XXVI–XXVIII. Armature formula: [1, 1, 11, 8, 1, 14+ae, 4, 3, 8]. Segment 6 very swollen with a complicated pattern of ridges and teeth on anterior surface (Fig. 10C–D). Segment 7 with 4 setae, 3 of which sagittiform, on anterior surface (Fig. 10E).

P1. Coxa with fewer spinule rows on anterior surface. Inner spine on basis without spinule row at base; inner spine less well developed and with finer spinules (Fig. 5E) than in female (Fig. 5D). Segments of both rami (Fig. 5B) more elongate than in female. Spinules on outer and distal margin of endopod segments much finer than in female, particularly on distal margin of enp-1 (Fig. 5C).

P2 (Fig. 6B–C). Basal pedestal and articulating surface of endopod enlarged. Enp-1 much larger than in female and inner seta transformed into a non-articulating process with a flagellate tip; outer spinules small. Enp-2 without inner seta or spinule row on outer margin; outer distal corner attenuated into an apophysis reaching well beyond the distal margin of enp-3. Enp-3 (Fig. 6C) reduced in size with no outer spinule row; outer distal spine shorter but stouter than in female with spinules reduced to coarse blunt teeth; terminal and inner setae also reduced in size compared to female.

P3 endopod (Fig. 7B–C). Enp-2 without outer spinule row; outer and inner distal corners much more attenuated than in female, apophysis at outer corner with hooked tip (Fig. 7C); inner seta much smaller than in female.

P5 (Fig. 11B). Baseoendopods of each leg fused medially; not fused to exopod. Endopodal lobe reduced with 2 pinnate setae of very unequal length. Exopod with 5 pinnate setae, inner seta small, middle seta longest.

P6 a single plate fused to somite proximally (Fig. 11A), with 3 pinnate setae on each side (Fig. 11C).

REMARKS

(i) Synonymy

The Alaskan material on which the above redescription is based, was first described in detail in an excellent paper by

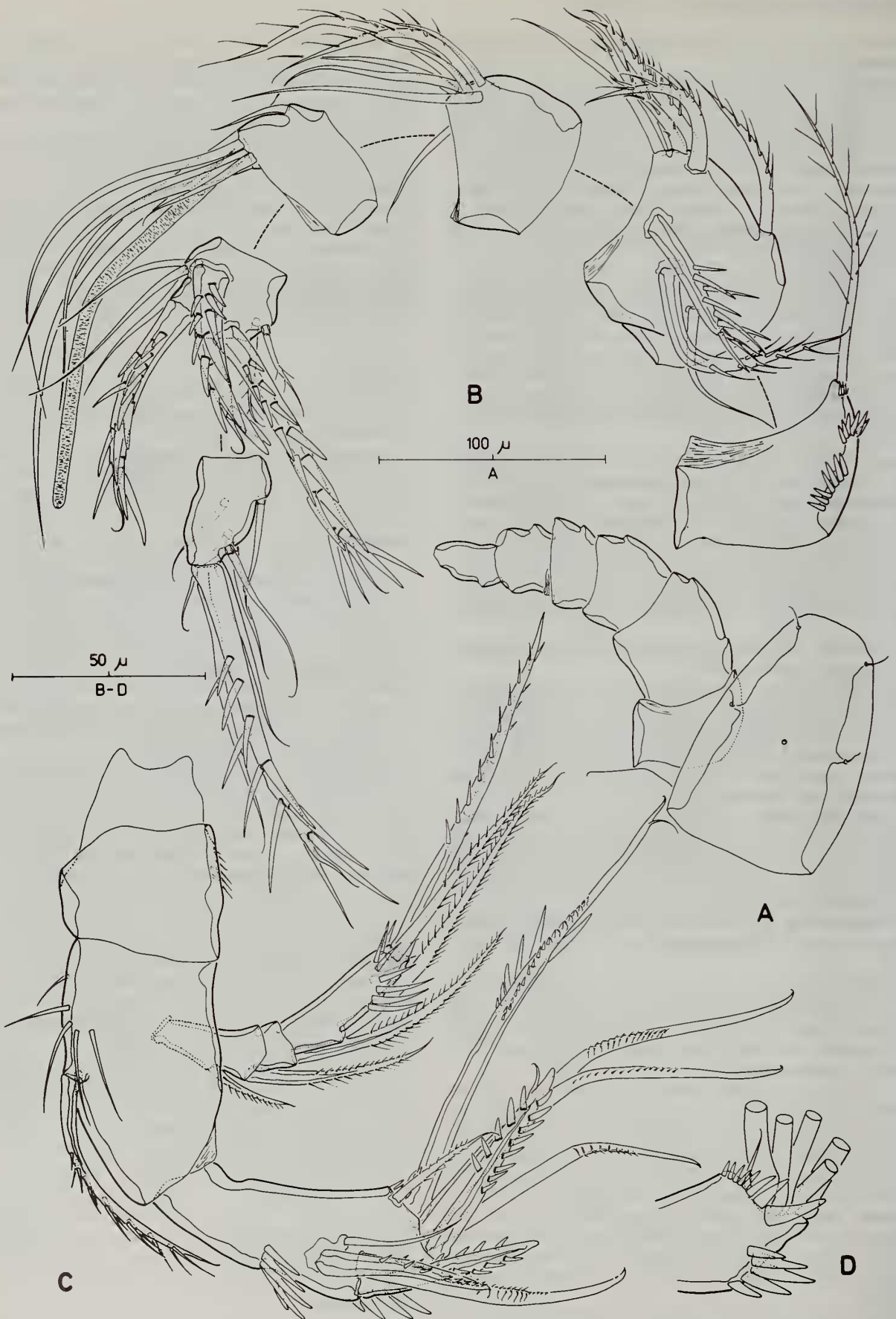


Fig. 2 *Archisenia sibirica* comb. nov. A, Rostrum and female antennule (armature omitted); B, female antennule (disarticulated); C, antenna, anterior view; D, antennary endopod, posterior view of distal margin.

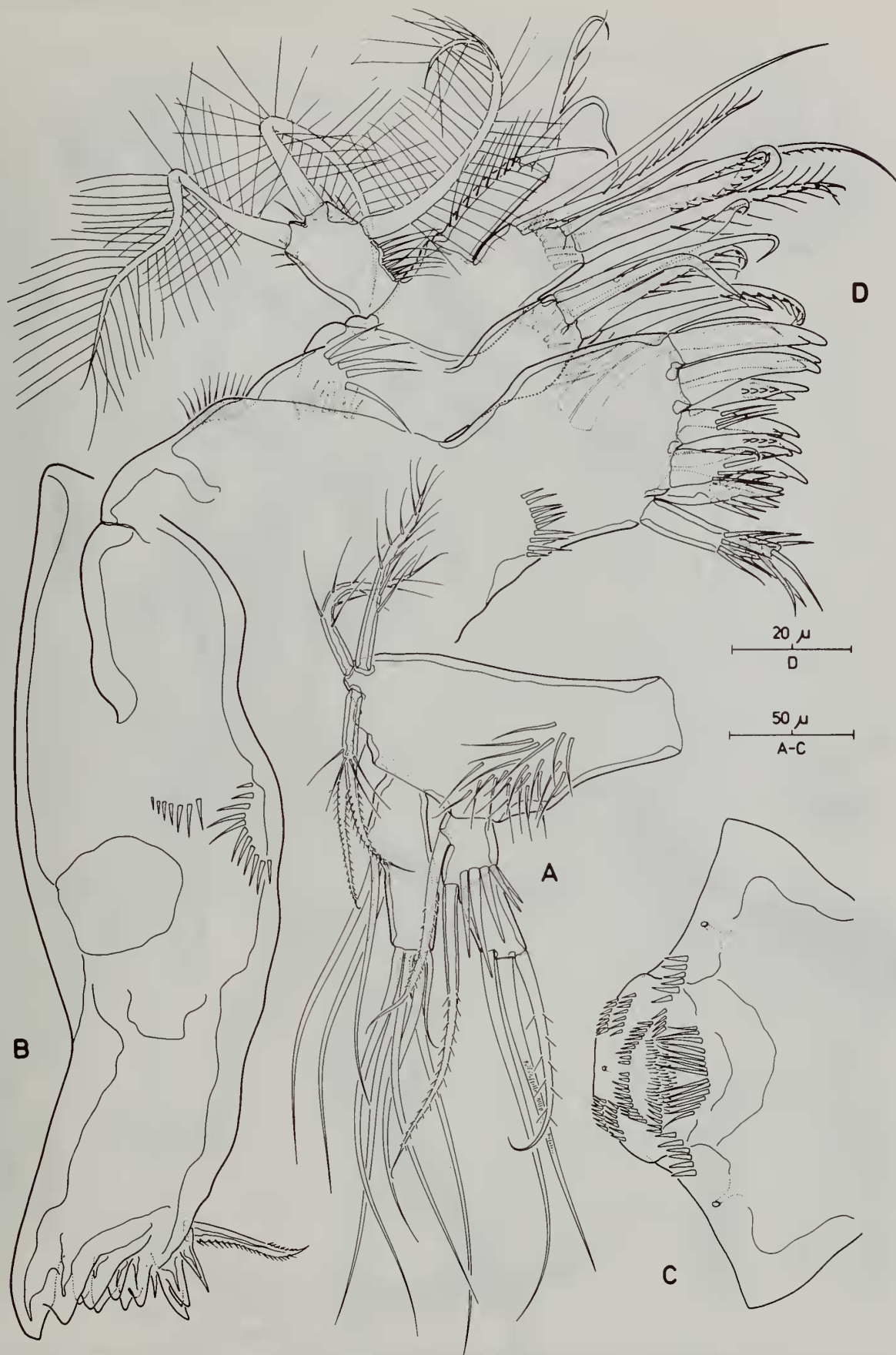


Fig. 3 *Archisenia sibirica* comb. nov. A, Mandibular palp; B, mandibular gnathobase; C, labrum; D, maxillule.

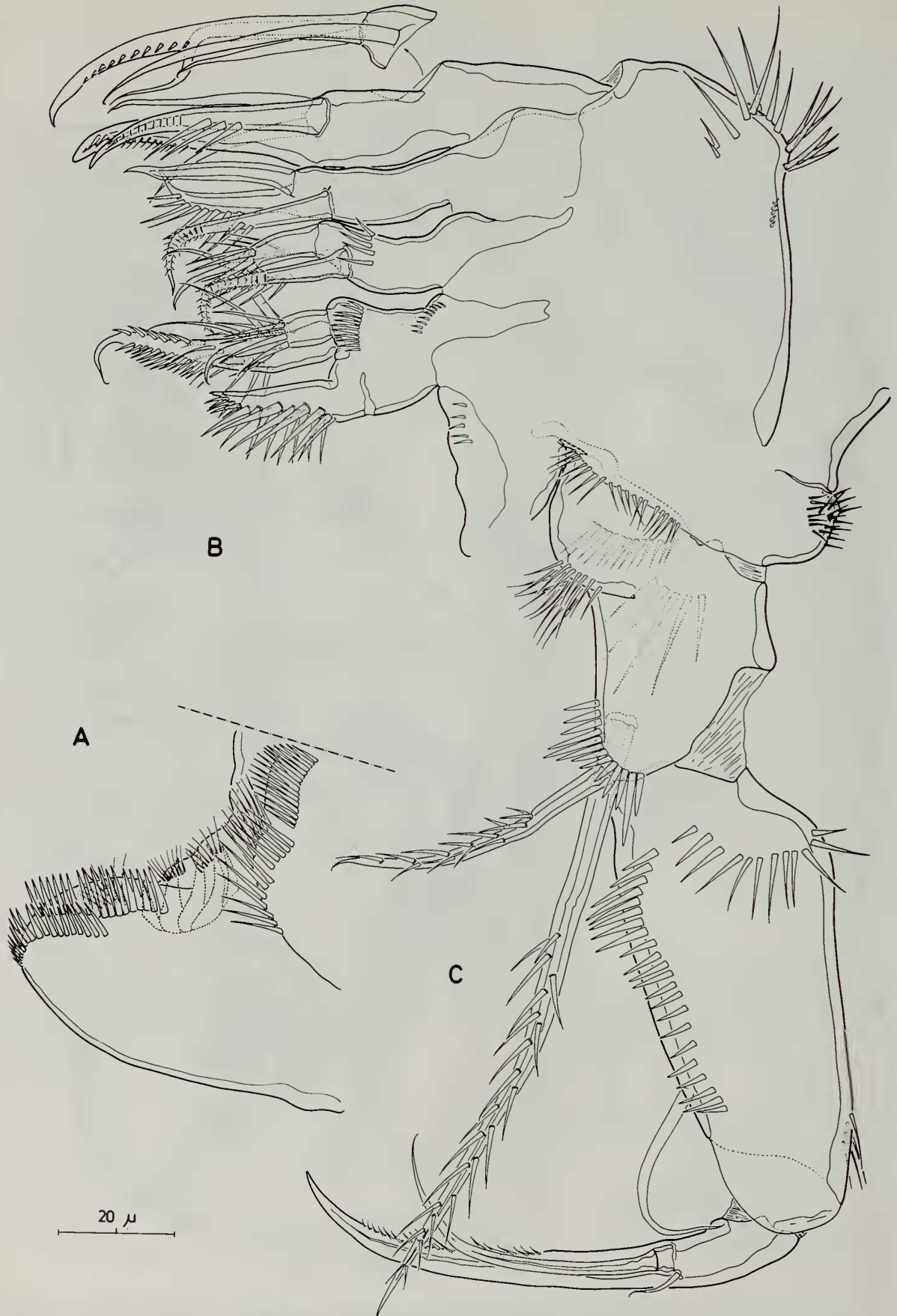


Fig. 4 *Archisenia sibirica* comb. nov. A, Right paragnath, posterior view; B, maxilla with disarticulated endopod; C, maxilliped.

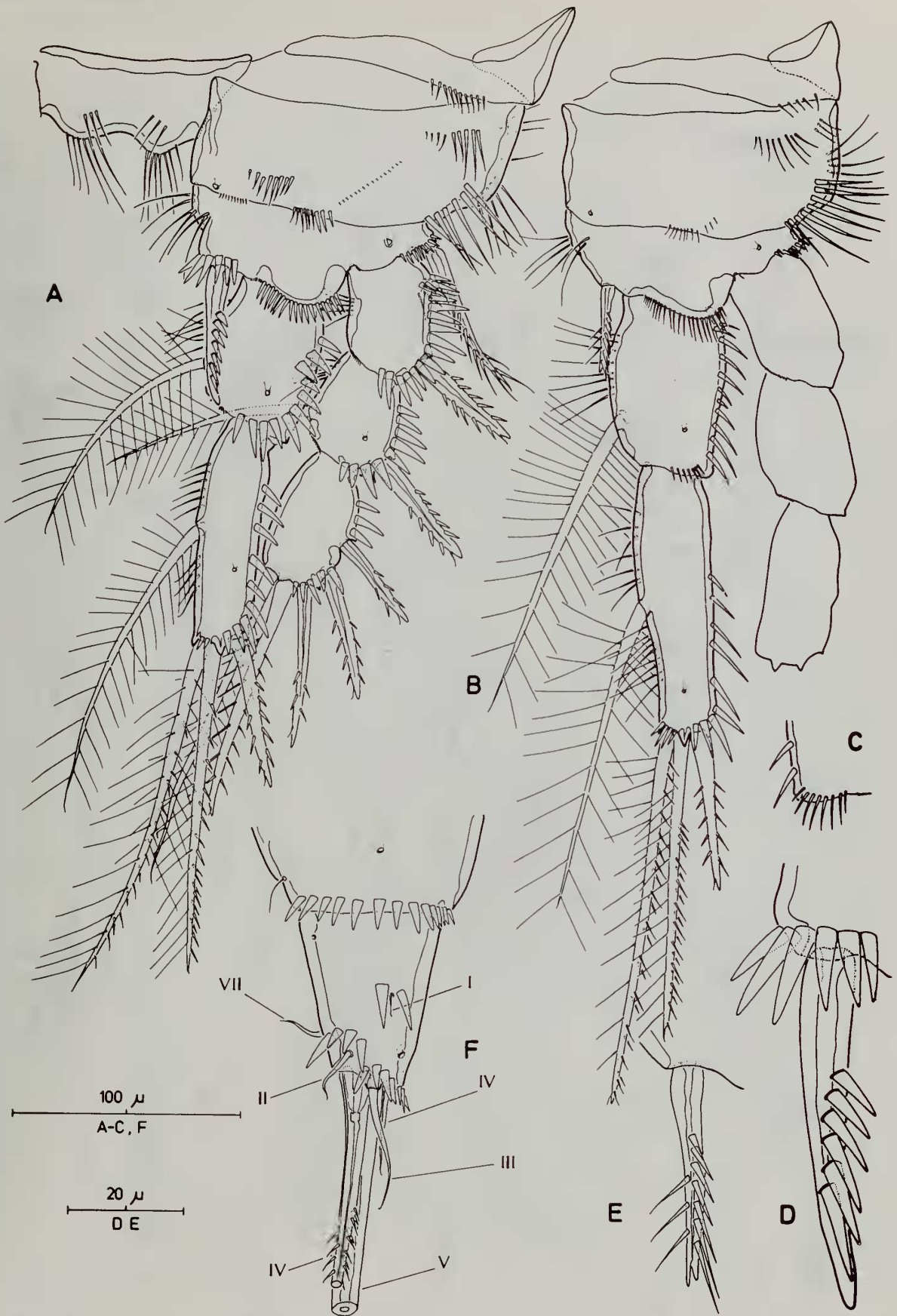


Fig. 5 *Archisenia sibirica* comb. nov. A, Female P1, anterior view; B, male P1, protopod and endopod, anterior view; C, male P1, distal margin of enp-1 of other side; D, female P1 inner basal spine; E, male P1 inner basal spine; F, caudal ramus, lateral view.

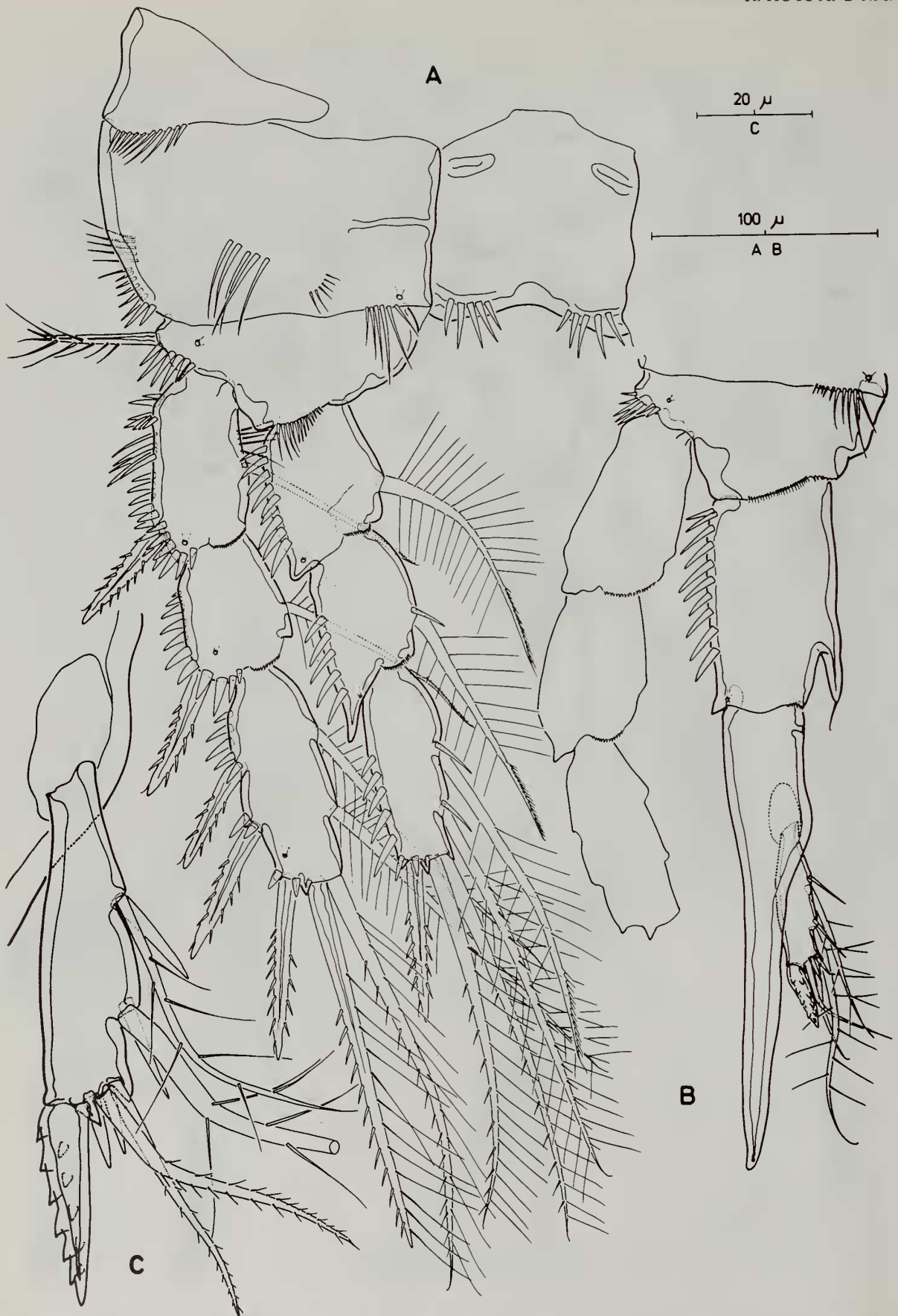


Fig. 6 *Archisenia sibirica* comb. nov. A, Female P2, anterior view; B, male P2 basis and endopod, anterior view; C, male P2 endopod distal segment, posterior view.

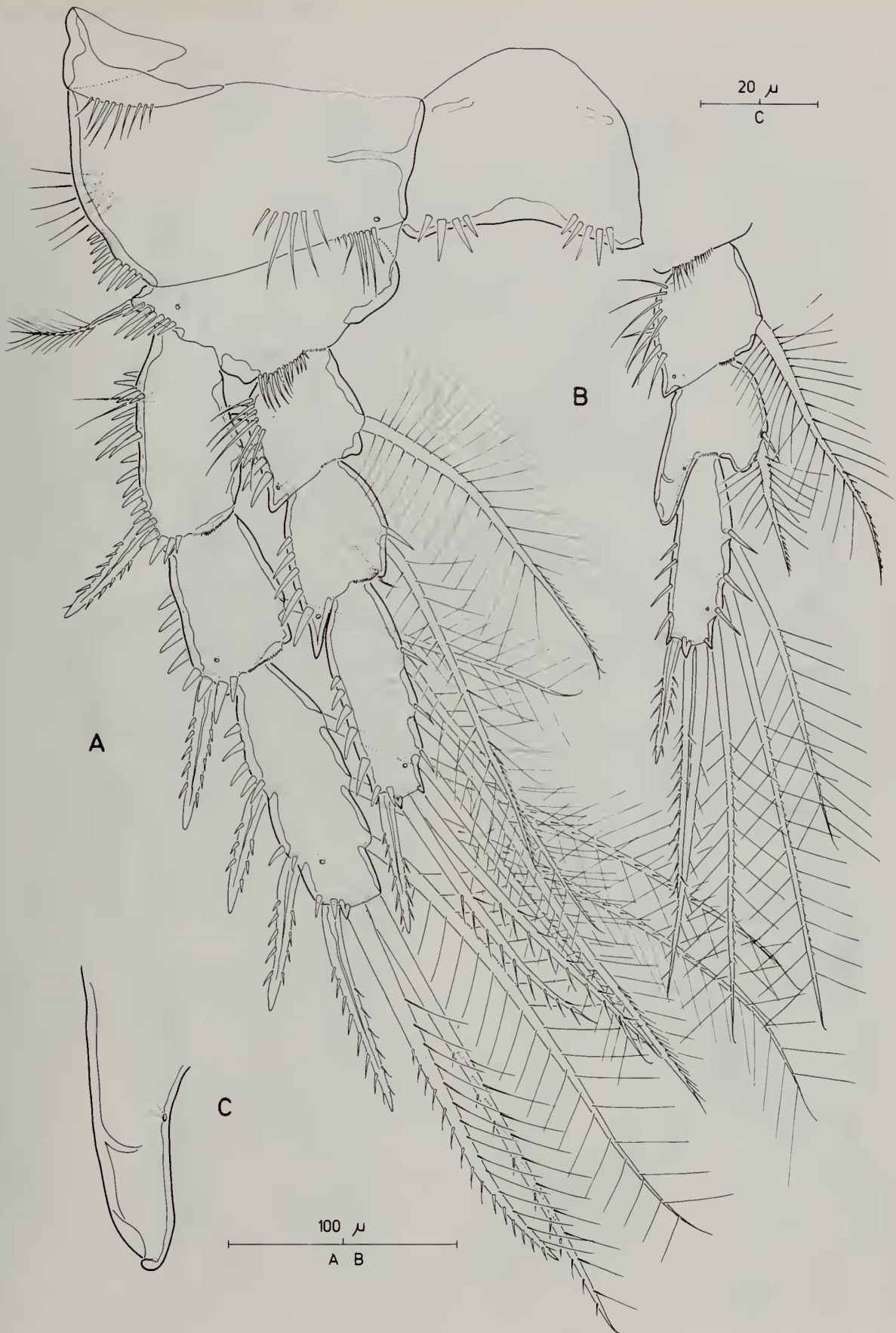


Fig. 7 *Archisenia sibirica* comb. nov. A, Female P3, anterior view; B, male P3 endopod, anterior view; C, male P3, detail of outer apophysis of enp-2.

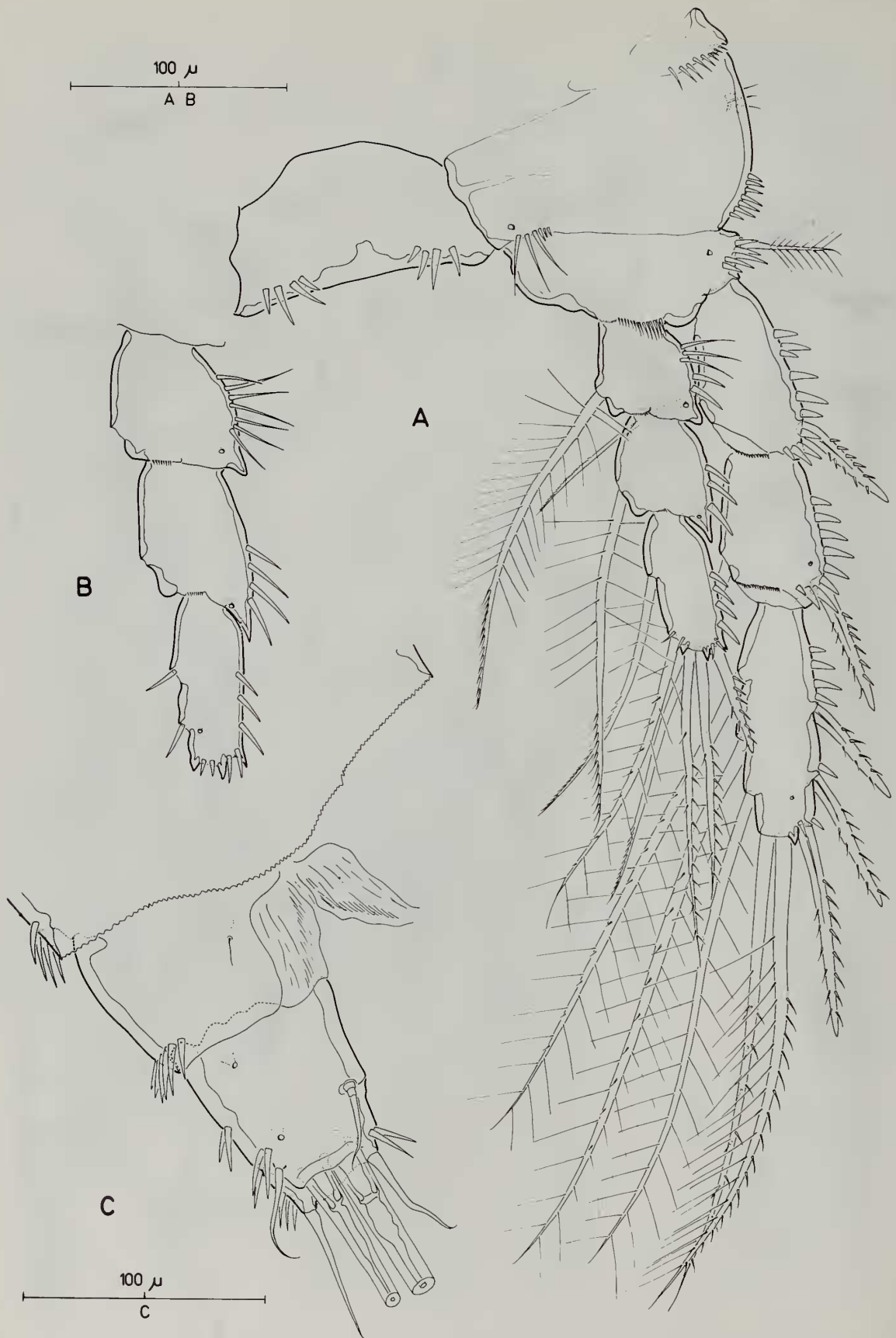


Fig. 8 *Archisenia sibirica* comb. nov. A, Female P4, anterior view; B, male P4, contours of endopod; C, pseudoperculum, anal somite and left caudal ramus in dorsal view.

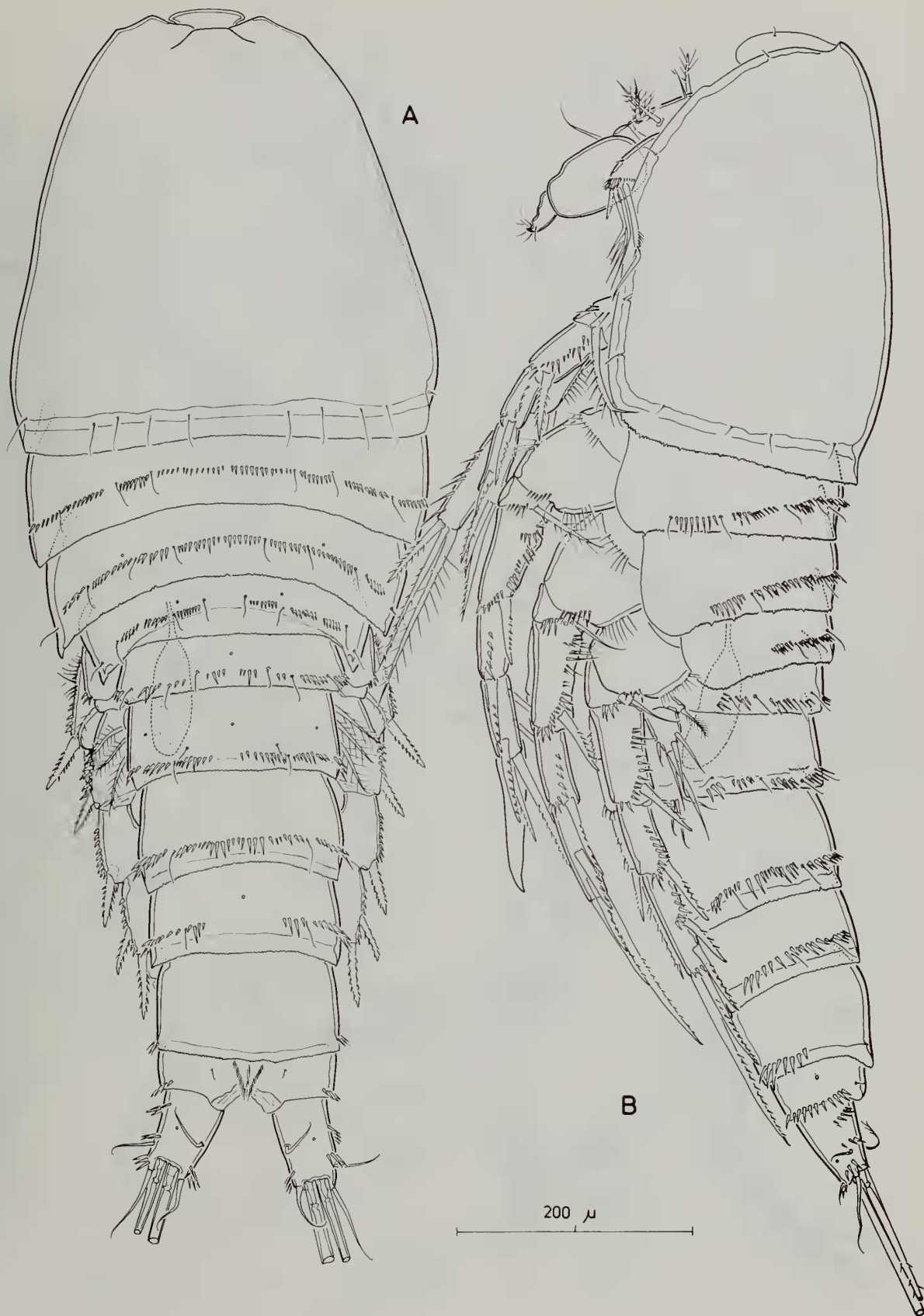


Fig. 9 *Archisenia sibirica* comb. nov. A, Male habitus, dorsal; B, same, lateral. [Sensillae on cephalothorax omitted.]

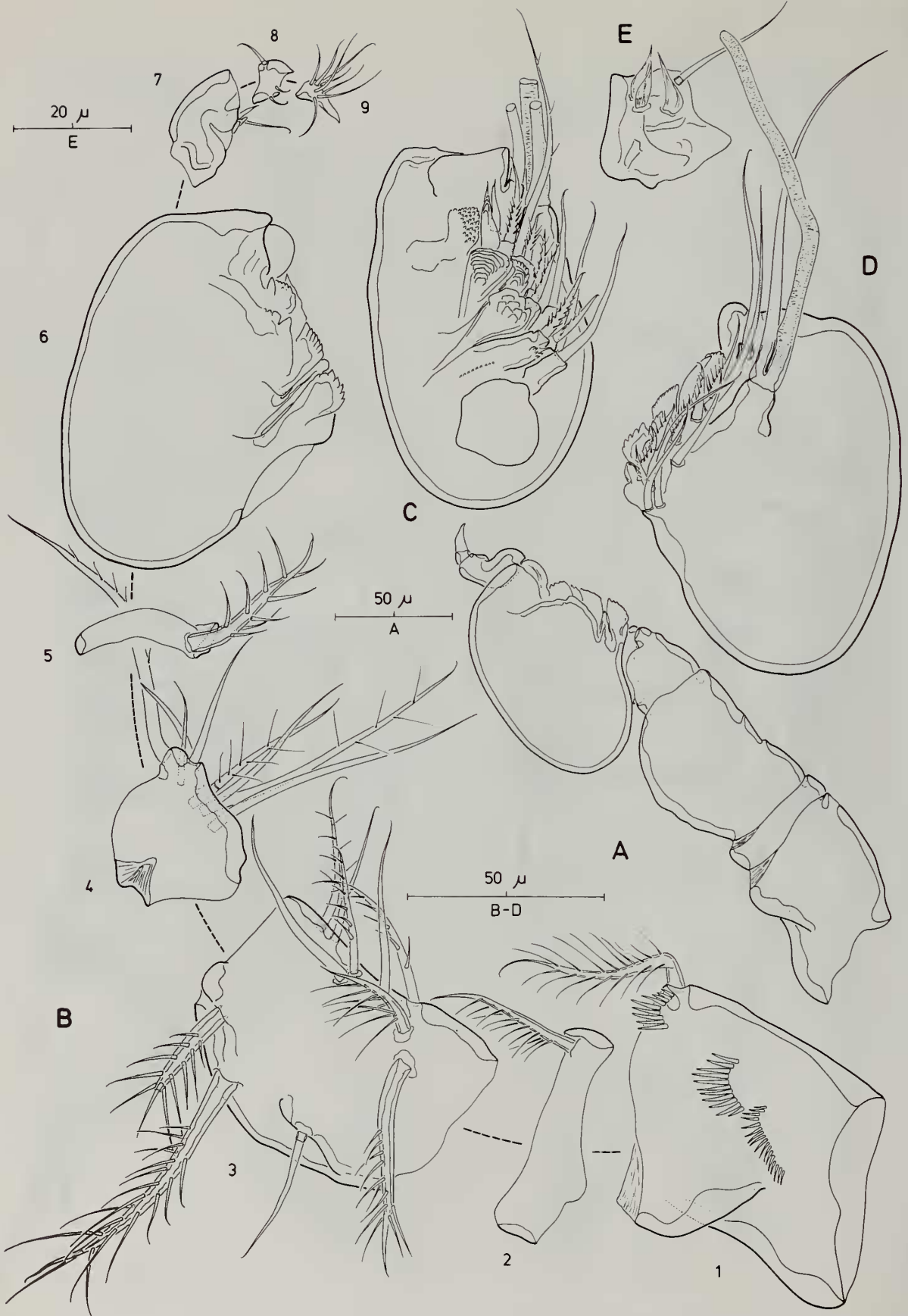


Fig. 10 *Archisenia sibirica* comb. nov. A, Male antennule (armature omitted); B, male antennule, disarticulated (armature of segment 6 omitted); C, male antennule segment 6, anterior view; D, same, ventral view; E, male antennule segment 7, anterior view.

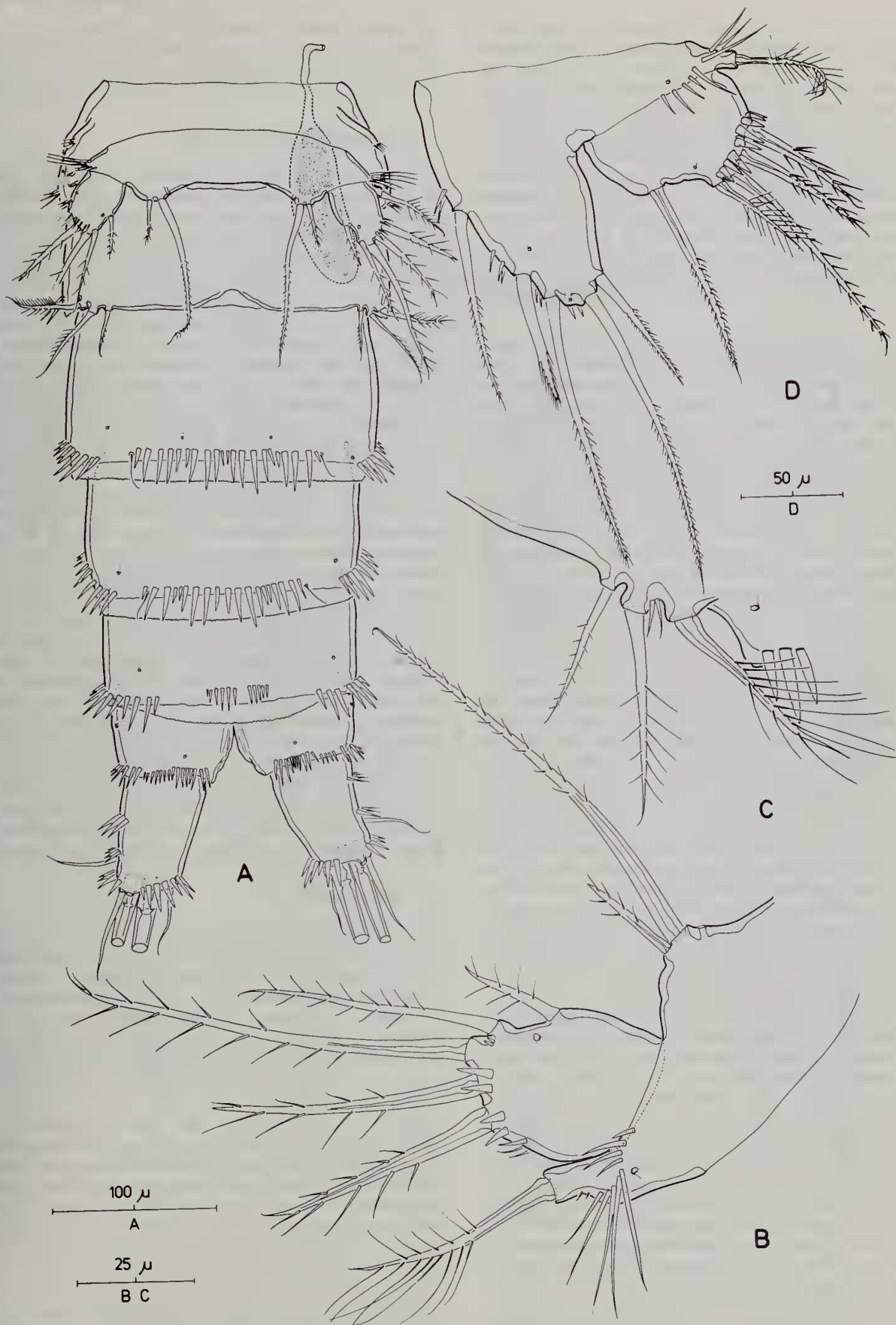


Fig. 11 *Archisenia sibirica* comb. nov. A, Male urosome, ventral view; B, male P5; C, male P6 armature; D, female P5.

Wilson (1966). There are slight discrepancies between these 2 descriptions which should be noted because of their possible phylogenetic significance. The rostrum does articulate with the cephalothorax and there are 2 accessory setae at the base of the maxillipedal claw. In the female there is no aesthetasc on the terminal segment of the antennule and the outer distal corner of enp-2 in P2 and P3 is significantly attenuated but that of enp-1 is normal (especially compared to the condition in *Psammis*). In the male the antennule is distinctly 9-segmented with segment 6 being swollen and bearing an aesthetasc; the distal outer element of P2 enp-3 is not completely fused to the segment but articulates along the anterior surface and partially articulates on the posterior surface; and there is no sexual dimorphism in P4 enp-2 (Fig. 8B).

We have been unable to locate the type, or any other, material of *D. sibirica* and therefore, like Wilson (1966), have had to rely on Sars' (1898) original description and figures. A study of these has led us to conclude that there are no real differences between *D. stefanssoni* and *D. sibirica*. We agree with Wilson's interpretation of the swimming leg setation. The original copy of Sars' paper in our possession also shows faint lines where the seta should be on P2-P4 exp-1 and in no other species in any paranannopid genus is this seta absent in the female when it is present in the male. Although Sars (1898) states in his text that the female antennule is 5-segmented, close scrutiny of his drawing (Plate X, Fig. 4) reveals that the terminal segment is at least partially divided into two segments and that the arrangement of the pectinate spines (3 on segment 5 and 1 at the apex of segment 6) is exactly the same as in *D. stefanssoni*. Further Sars has clearly misinterpreted the segmentation of the male antennule in that he has combined segments 1 and 2 as shown by the fact that his segment 1 bears 2 setae, a condition found in no other Paranannopidae. Wilson (1966) concluded that the only real difference between *D. stefanssoni* and *D. sibirica* was the absence in the latter of the distinctive outer distal spine on P2 enp-3 in the male. However, Sars' drawing of this limb (Plate X, Fig. 16) shows only 4 elements on enp-3 instead of 5, as in the female, and it is possible that the crucial one (the outer spine) is concealed behind the large apophysis on enp-2. This interpretation is supported by the fact that, irrespective of the degree of modification in males, the number of elements on P2 enp-3 is always the same in both sexes, except in the genera bearing claviform aesthetascs on the mouthparts (Gee & Huys, 1991) where the distal outer spine is further modified into a non-articulating apical apophysis.

These observations, coupled with such factors as similarity of size (they are the largest known members of the Paranannopidae except for *Psammis borealis* Klie, 1939 whose taxonomic position is unclear) and the peculiar identical distribution of setae on the distal margin of the female P5, lead us to the conclusion that the two species are synonymous and have a circum-polar distribution. Fig. 13 shows that the most easterly record of *D. sibirica* at Wrangell Island (Yashnov, 1935) is very close to the most westerly record of *D. stefanssoni* on the Chukchi Sea coast of Alaska (Wilson, 1966). The only record of the species outside the Arctic Circle is that of Wells (1965) from Loch Nevis on the west coast of Scotland and this must be regarded as doubtful (original specimens no longer available for re-examination). Further, both *D. stefanssoni* and *D. sibirica* have been recorded from estuaries and in brackish water, a most unusual habitat for members of this family. All other species are found only in

sublittoral marine habitats although *Danielssenia typica* Boeck, 1872, the other species with a known global distribution, has been recorded from the Baltic Sea (Veldre & Mäemets, 1956; Arlt, 1983), a region of lowered salinity.

(ii) Autapomorphies of *Archisenia*

Turning now to consider the taxonomic status of *D. sibirica*, its distinction from other members of the genus *Danielssenia* was suggested by Lang (1944) who divided *Danielssenia* into 2 groups, the *typica* group and the *sibirica* group. The latter he characterized by: (i) antenna exp-1 with 2 setae; (ii) P4 enp-3 with 2 inner setae; (iii) the male P2 enp-1 with the inner seta transformed into a non-articulating process; (iv) the male P3 enp-2 with an outer hooked apophysis. This last character is now known to occur in all species of Paranannopidae and might even be a diagnostic character for a wider group of families. The first two characters, although diagnostic of *D. sibirica* in combination, are the plesiomorphic condition in the family and are found in a number of other genera. *Paranannopus*, *Psammis*, *Micropsammis* Mielke, and *Bathypsammis* gen. nov. also retain 2 setae on exp-1 of the antenna (all other genera bear only 1 seta on this segment) and *Sentirenia* Huys & Gee (= *Jonesiella* Brady, see below) and the male of *Fladenia* retain 2 inner setae on P4 enp-3. However, the transformation of the inner seta into a non-articulating spine on P2 enp-1 in the male is unique to this genus, as are the following autapomorphies: (i) the outer extension on P3 enp-2 in both sexes; (ii) the sigmoid, heavily sclerotized female copulatory duct; (iii) the sexual dimorphism of the inner basal spine of the male P1. Another character of phylogenetic significance is the loss of the inner seta on the male P2 enp-2. This character is also found in *Afrosenia spinipes* (Wells, 1967) and is regarded here as a product of convergence. A further character which is unique but difficult to quantify is the arrangement of the setation on the exopod of P5, with the inner seta well separated from the remaining setae. It is on the basis of all these characters that we have removed *D. sibirica* to a new genus leaving the *typica* group as the only species group in the genus *Danielssenia*.

(iii) Intersexuality

The male from East Greenland (Fig. 12), collected by Jespersen, proved upon examination to be an aberrant intersexual specimen. It has the male body facies, including a 6-segmented urosome (Fig. 12A), a well developed testis and vas deferens (however, a spermatophore has not been observed), and the male form of the P5 and P6. The endopods of P2 and P3 are also modified but differ from the typical male condition by the retention of certain female features.

The antennules resemble the female condition in all aspects: they are 6-segmented, lack any trace of a geniculation mechanism and possess the female armature pattern. The P1 (Fig. 12B) basis and endopod show the same spinule arrangement as in the female but size and shape of certain spinule rows approach the male condition. The P2 endopods are not identical on both sides (Figs. 12C-D) and show a combination of male and female characteristics. The proximal segment and its basal pedestal are moderately enlarged but the spinule at the base resembles the female condition and the inner seta is — though being shorter than in the female — not transformed into a spinous process. The outer apophysis

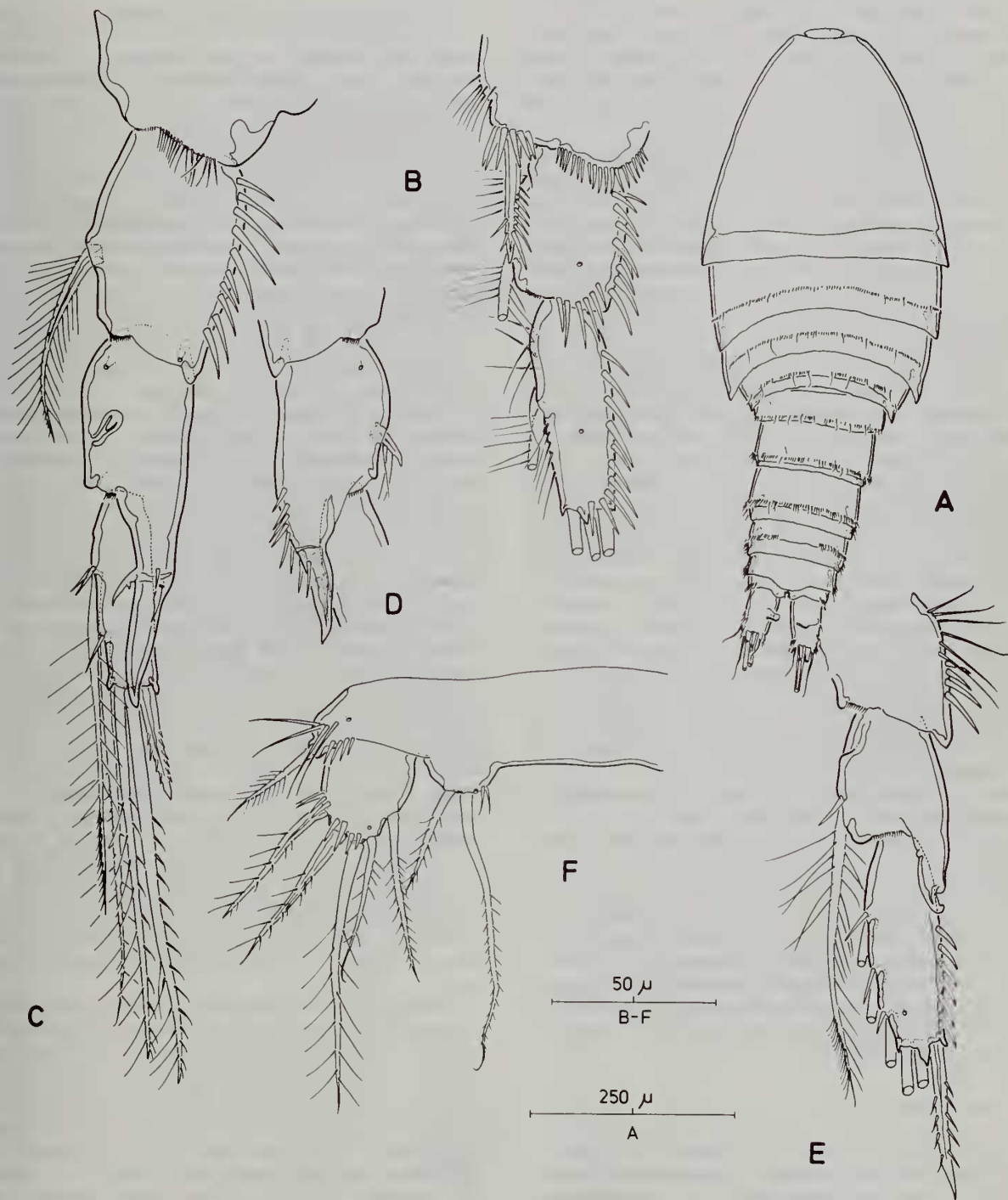


Fig. 12 *Archisenia sibirica* comb. nov. Intersex specimen from Greenland. A, Habitus, dorsal view; B, P1, endopodal segments; C, P2, endopod of right side; D, P2, middle endopod segment of left side; E, P3 endopod; F, P5.

of the middle segment is distinctly shorter than in the typical male and its outer margin might bear spinules as in the female; the inner seta — completely missing in the male — is represented by a vestigial spine which is either entirely (Fig. 12C) or partly (Fig. 12D) invaginated. The distal segment is almost identical to the female condition. The P3 endopod is modified as in the male except that the inner seta of the middle segment is distinctly longer than in the typical male (but shorter than in the female). The P4 endopod grossly resembles the male condition. The P5 also has the basic male outline but the endopodal lobe is slightly more pronounced and the inner exopodal seta is distinctly longer.

Intersexuality within the Harpacticoida appears to be very rare. Klie (1944) describes a female specimen of *Amphiascoides debilis* (Giesbrecht, 1881) from Helgoland which displayed the male condition for the antennules (i.e. haplocer) and the first thoracopods (i.e. modified basis) and the female condition for the genital somite and the remaining appendages except for the P2 endopod which combined both male and female features. Recently, Moore & Stevenson (1991) found that 90% of a population of *Paramphiascella hyperborea* (T. Scott, 1903) in the vicinity of a sewage outfall in the Firth of Forth, Scotland, were intersex specimens. In the majority of these the prosome (including the antennules and swimming legs) exhibited the female condition whilst the urosome had the male condition of 6 distinct somites and a plate-like P6, although the P5 was more similar to that of the female. At the same site, a small number of intersex specimens of *Stenhelia gibba* Boeck, 1864 and *Halectinosoma similidistinctum* Lang, 1965 were also found. Intersexuality is more common in other orders of copepods, particularly the calanoids *Eudiaptomus vulgaris* (Schmeil, 1898), *Arctodiaptomus (Rhabdodiaptomus) alpinus* (Imhof, 1885), *Eudiaptomus gracilis* (Sars, 1863), *Pseudocalanus elongatus* (Boeck, 1864), *Calanus hyperboreus* Krøyer, 1838, *Paracalanus parvus* (Claus, 1863) (Bremer, 1914; Pirocchi, 1940; Cattley, 1949; François, 1949; Conover, 1965; Ianora *et al.*, 1987) and cyclopoids *Megacyclops gigas* (Claus, 1857) and *Megacyclops viridis* (Jurine, 1820) (Mrázek, 1913; Coker, 1938).

In natural populations the frequency of occurrence of intersexuality appears to be very low and may be a result of infrequent chromosomal aberrations during embryonic development. In cases of higher incidence, various causes of intersexuality have been postulated. Coker (1938) attributed it to low temperature during naupliar development; Cattley (1949) to parasitism of the developmental stages by the marine ectoparasitic dinoflagellate *Blastodinium contortum hyalinum* Chatton; and Moore & Stevenson (1991) argued that the very high incidence of intersexuality in the vicinity of a sewage outfall strongly implicated some form of chemical pollution as the causative factor.

Genus *Danielssenia* Boeck, 1872

Since the publication of Lang's (1948) monograph a number of new species have been assigned to the genus *Danielssenia* but recent analyses have shown this to be a heterogeneous assemblage. In previous papers (see also Table 1) we have removed *D. intermedia* Wells, 1965 to the genus *Fladenia*; *D. perezi* Monard, 1935 (syn. *D. paraperezi* Soyer, 1970) and *D. eastwardae* Coull, 1971 to the genus *Sentirenia* and propose to remove *D. spinipes* Wells, 1967 and *D. minuta* Coull, 1969 to two other new genera (Gee & Huys, 1990; Huys & Gee, 1992, in press). This has restricted the genus *Danielssenia* to

the following species: *D. typica*; *D. quadriseta* Gee, 1988; *D. reducta* Gee, 1988; *D. robusta* Sars, 1921 and *D. similis* Chislenko, 1971. The status of *D. fusiformis* (Brady, 1880), previously been synonymized with *D. typica* (cfr. Shen & Bai, 1956; Gee, 1988b) is reconsidered here.

(i) *Danielssenia fusiformis* (Brady, 1880) nec Sars (1910)

Brady (1880) created the genus *Jonesiella* to accommodate two new species, *J. fusiformis* (Brady & Robertson) and *J. spinulosa* (Brady & Robertson), and provided illustrated descriptions for these species. Brady remarked that both species had already been listed in an earlier report (Brady & Robertson, 1876) as *Zosime* (?) *fusiformis* and *Z. spinulosa*, respectively, and therefore unjustly concluded that both authors had to be credited with the authorship. This state of affairs has perpetuated in the nomenclature, even to the present (e.g. Gee, 1988b), though it is clear that Brady & Robertson's species names are mere *nomina nuda* and only Brady (1880) should be cited as the author of both *Jonesiella* species. Norman & Scott (1906) were the first to list *J. spinulosa* Brady, 1880 as a junior synonym of *Danielssenia typica* Boeck, 1872 and also changed *J. fusiformis* Brady, 1880 into *D. fusiformis*. Both species were redescribed and illustrated by Sars (1910) who admitted that they were very similar. It were also Sars' descriptions that led Shen & Bai (1956) to conclude that both species were identical, and after careful examination of Sars' material Gee (1988b) formally relegated *D. fusiformis sensu* Sars (1910) to a junior synonym of *D. typica*. There is, however, considerable evidence that what Sars (1910) considered to be *D. fusiformis* in Norway is clearly different from Brady's (1880) original material from the Scilly Islands. Brady's type material does no longer exist, but his illustrations (Plate XLVIII, Figs 1–13) of the female antennule, mandible, maxilliped, P1, the fifth legs in both sexes and the male endopod P2 leave no doubt that his species is identical with *D. perezi* Monard, 1935, originally described from Roscoff and later also recorded from the Scilly Islands (Wells, 1968) — the type locality of *J. fusiformis*. Huys & Gee (1992) recently synonymized *D. paraperezi* Soyer, 1970 with *D. perezi* and established a new genus *Sentirenia* to include the latter species and *D. eastwardae* Coull, 1971. *Sentirenia* Huys & Gee, 1992, therefore, has to be relegated to a junior synonym of *Jonesiella*, thus encompassing the type species *J. fusiformis* Brady, 1880 nec Sars (1910) (syn. nov.: *Danielssenia perezi* Monard, 1935; *D. paraperezi* Soyer, 1970) and *J. eastwardae* Coull, 1971 comb. nov.

Thompson's (1893) illustration of the female antennule suggests that his record of *J. fusiformis* from Liverpool Bay is correct. Re-examination of specimens (7 ♀♀ labelled *D. fusiformis*; Norman collection, reg. no. 1911.11.8.43561-565, gift from T. Scott; October 1899) collected in the Firth of Clyde indicates that the species might be distributed along the entire west coast of Britain. Lang's (1936a,b) specimens from the Öresund and Spitzbergen clearly belong to *D. typica*. All other records of *D. fusiformis* have to await confirmation (see list in Lang, 1948).

(ii) *Danielssenia robusta* Sars, 1921

Lang (1948) was of the opinion that *D. robusta* (and *D. perezi*) probably would require the definition of additional species groups inside the genus but as the males were still

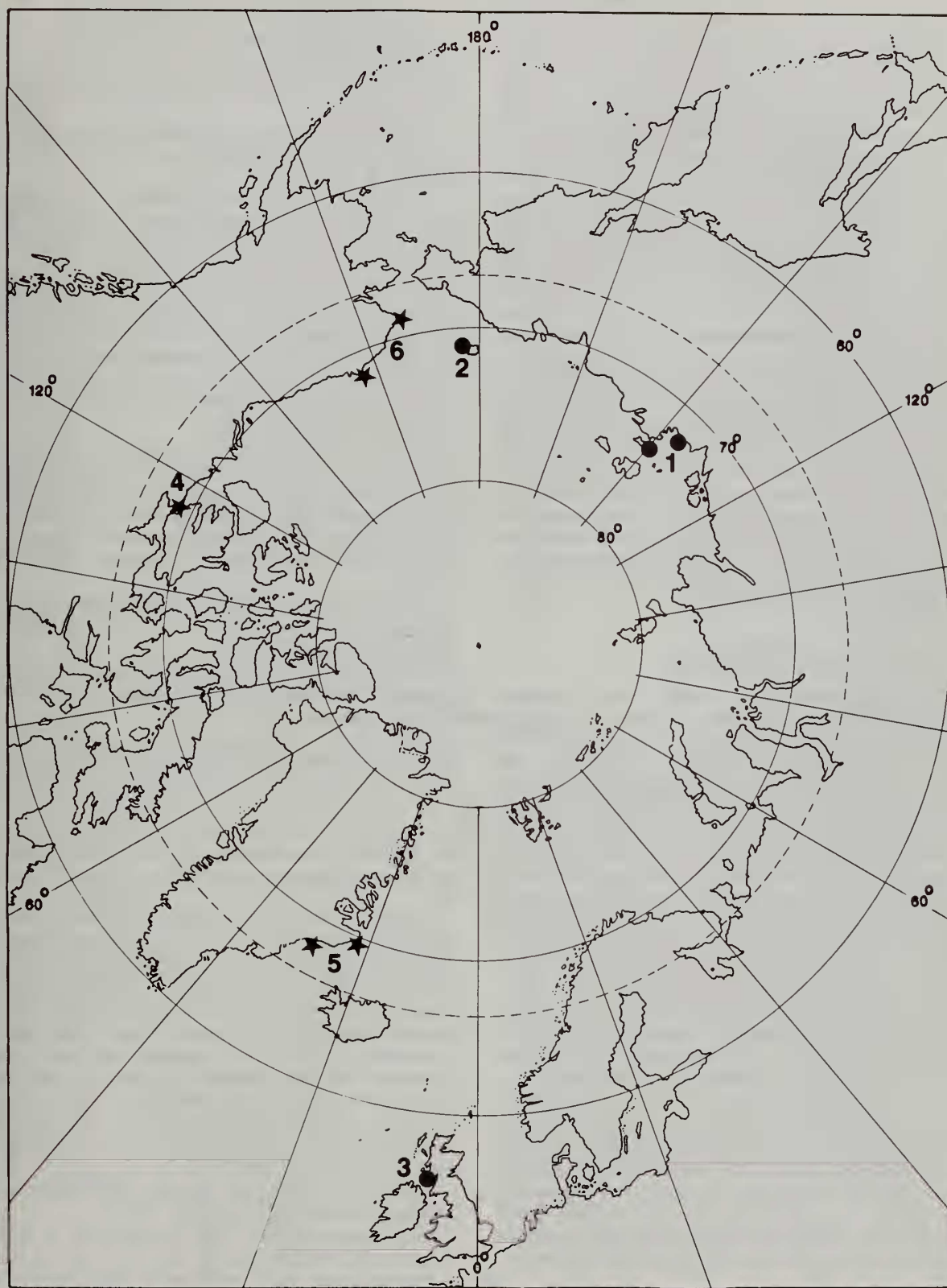


Fig. 13 Distribution map of *Danielssenia sibirica* (circles) and *D. stefanssoni* (stars). Records of 1. Sars (1898); 2. Yashnov (1935); 3. Wells (1965); 4. Willey (1920); 5. Jespersen (1939); 6. Wilson (1966). Arctic Circle shown by dashed line.

unknown at that time he regarded such an allocation as being premature. We have re-examined Sars' material of this species from Risør, Norway (13 ♀♀ and 1 copepodid V stage; Zoologisk Museum, Oslo, Reg. No. F20257) and found the following significant discrepancies from the original description of Sars (1921): (i) there is an inner seta on exp-1 of P2-P4; (ii) the inner element on enp-1 of P2-P4 is a pinnate spine; (iii) the P5 baseopod has 4 setae, the second inner one being much smaller than the others; (iv) the P5 exopod is fused to the baseopod on the posterior surface. Further, we have made a detailed comparison of these females with the recently discovered female of *D. intermedia* (which was assigned to the genus *Fladenia* by Gee & Huys (1990)) and have found them to be identical. Therefore *D. robusta* must be referred to the genus *Fladenia* whose type species now becomes *F. robusta* (Sars, 1921) comb. nov. as this has priority over *F. intermedia* (Wells, 1965). *F. robusta* has also been recorded from the Mediterranean by Por (1964), who found one female in 470 m off the coast of Israel, and Soyer (1970) who found 18 adult females at depths ranging from 50 to 420 m in the vicinity of Banyuls-sur-mer. Both authors state in their text that these specimens agree exactly with the original description. However, Por's (1964) Fig. 73 does show an inner seta on exp-1 of what is probably P4 (this limb is labelled P1 by Por but cannot possibly be so as the endopod is 3-segmented). This, taken in conjunction with his figure of the P5 (1964, Fig. 74) leaves little doubt that the Mediterranean material can be assigned to *F. robusta*, thus giving this species a Boreo-Mediterranean distribution similar to that of *Jonesiella fusiformis* (see Huys & Gee, 1992).

(iii) *Danielssenia similis* Chislenko, 1971

Chislenko (1971) distinguished *D. similis* from *D. typica* on the basis of the following characters: (i) Size, the specimen drawn in his Fig. 1 is approximately 0.9 mm long; (ii) a maxilliped with only 1 seta on the syncopa and a somewhat longer seta on the basis; (iii) the sexual dimorphism on P2 endopod, with the loss of the inner seta on enp-1 and of 1 seta on enp-3. The character of size is of no particular significance as it is within (but near the upper limit of) the size range of *D. typica* given by Gee (1988b). Similarly, the absence of a large seta on the basis of the maxilliped is of doubtful significance as this seta can be easily dislodged during dissection, as was the case in Sars' (1910) description of *D. typica* (see Gee, 1988b). The differences in sexual dimorphism of the male P2 endopod are more difficult to assess from drawings alone. However, it is highly improbable that the inner seta on P2 enp-1 is missing in the male when it is present in the female as this condition is found in no other member of this genus or indeed of the family as a whole. The same goes for a reduction in the number of setae on enp-3. In *Danielssenia*, the 2 terminal setae on this segment are very reduced and implanted close together and it is conceivable that Chislenko (1971) has combined these 2 fine setae and drawn them as one broad one. We believe that *D. similis* is referable to *D. typica* which has been shown to be the most variable species in the genus (Gee, 1988b) but without being able to examine topotype material we must regard it as a *species inquirenda*.

(iv) *Danielssenia typica* Boeck, 1872

The following material of the Norman collection (The Natural History Museum) has been examined (species name given

on the original museum label presented in parentheses):

1911.11.8.43451-470: vial containing > 400 specimens, mostly ♀♀, a gift from T. Scott; collected near Duke Buoy, Plymouth, 01 August 1889;

1911.11.8.43471-490: vial containing 23 ♀♀ and 1 ♂, a gift from T. Scott; collected from Varanger Fjord, East Finmark, Norway, 1890;

1911.11.8.43491-510: vial containing 31 ♀♀ and 3 ♂♂, a gift from T. Scott; collected from Vadsö, East Finmark, Norway, 03 July 1890;

1911.11.8.43511-530: vial containing 39 specimens (*D. typica*), a gift from T. Scott; collected in Trondhjem Fjord, Norway, 1893; 32 ♀♀ belong to *D. typica*, the other 7 ♀♀ belong to two different species of *Halectinosoma*;

1911.11.8.43531-540: vial containing 16 specimens (*D. typica*), a gift from T. Scott; collected from Inchkeith in Firth of Forth, October 1895. None of these specimens belongs to *D. typica*, instead the vial contained *Bradya* sp. (2 ♀♀, 8 copepodids), 2 ♂♂ *Robertsonia tenuis* (Brady & Robertson), 1 ♀ *Idomene coronata* (T. Scott) and 3 ♀♀ of a *Fladenia*-like paranannopid;

1911.11.8.43541-560: vial containing > 1000 specimens, mostly ♀♀, a gift from T. Scott; collected from Kames Bay, Isle of Cumbrae, 1888; a second lot of about 200 specimens from the same locality is registered under no. 1900.3.29.274;

1911.11.8.M.2299: 1 ♀ dissected on slide (*Jonesiella spinulosa*), dried out; collected in Trondhjem Fjord, Norway, 1893;

1911.11.8.M.2301: 43 specimens mounted *in toto* on slide (*Jonesiella spinulosa*), dried out; collected near Duke Buoy, Plymouth, 02 August 1889;

1911.11.8.M.2300: 8 specimens mounted *in toto* on slide (*Jonesiella spinulosa*), dried out; collected from Vadsö, East Finmark, Norway, 1890;

1900.3.6.644: 5 ♀♀ mounted *in toto* and 3 ♀♀ (one belonging to *Halectinosoma* sp.) dissected on slide (*Jonesiella spinulosa*); collected in Trondhjem Fjord, Norway, 1893.

Gee's (1988b) redescription of *D. typica* is updated here by the following observations and illustrations (Figs 14-16) based on specimens from Duke Buoy (closest to type locality):

Somatic hyaline frills of pedigerous and abdominal somites minutely dentate (Fig. 14A) except for the dorsal frill of P5-bearing somite which is deeply incised, forming rectangular lappets (Fig. 14A, B). Frill of cephalothorax smooth. Dorsal transverse spinule rows are found only on thoracic somites bearing P3-P5, the genital double-somite and second abdominal somite. Genital double-somite with continuous transverse chitinous rim dorsally, laterally and ventrally, marking original segmentation (Figs. 14A, D; 16D-E). Pseudopericulum (Figs. 14E-F) formed by deeply incised posterior extension of penultimate somite. Pattern of caudal rami setae as in Figs. 14E-F.

Rostrum (Fig. 16I) large, hyaline, with 2 pairs of minute sensillae; typically deflected (Figs. 14A-C).

Male antennule (Fig. 15G) 8-segmented or indistinctly 9-segmented; distal 2 segments very small and largely fused.

Mandible with blunt teeth and a single pinnate seta on gnathobase (Fig. 15A). Palp with short, equally long, 1-segmented rami (Fig. 15B); basis with row of very long setules proximally, inner margin with 1 short and 2 long setae; endopod with 2 lateral and 6 apical setae; exopod with

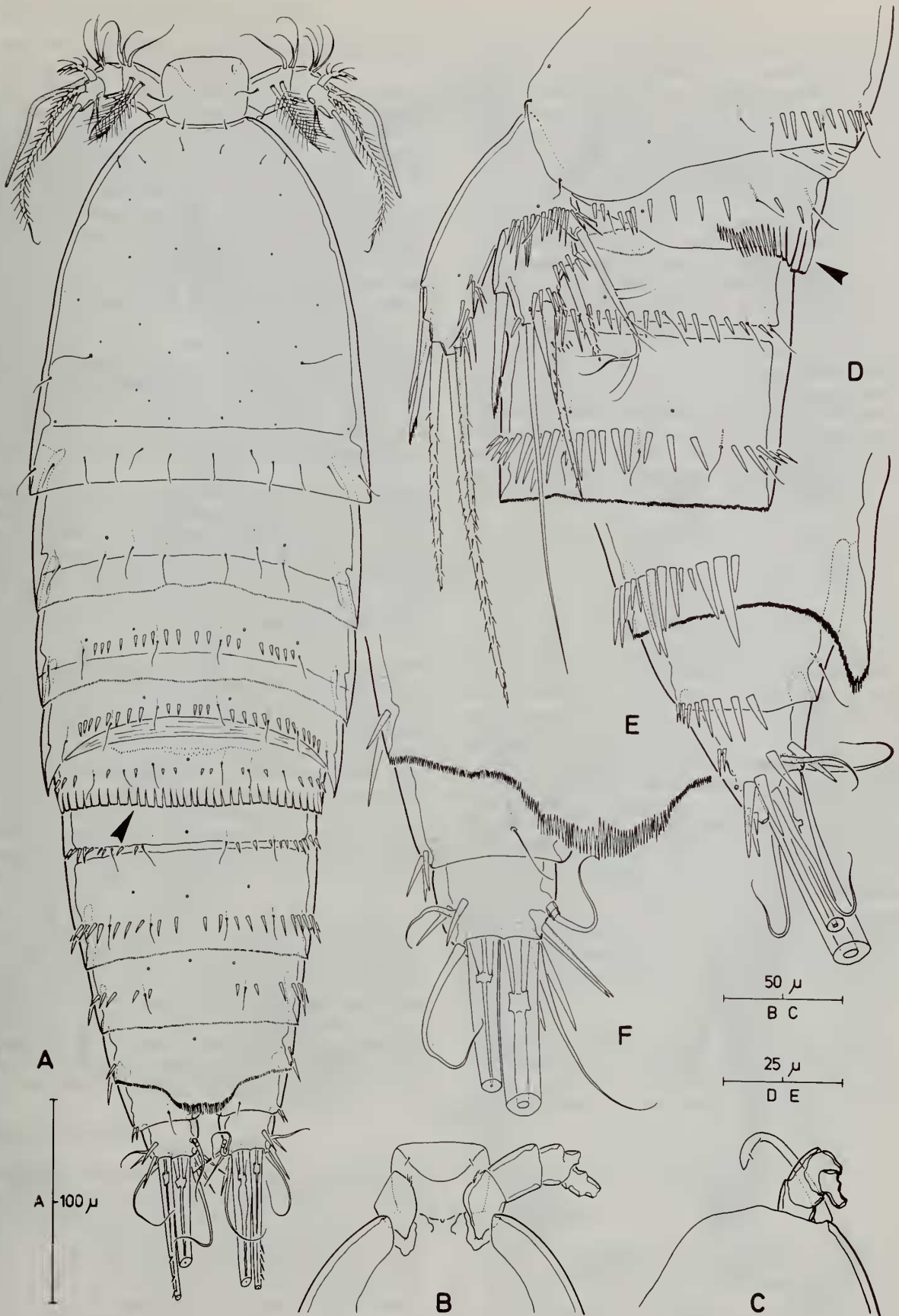


fig. 14 *Danielssenia typica*. Female: A, habitus, dorsal; B, rostrum and anterior part of cephalothorax, ventral; C, same, lateral; D, pleurotergite of P4-bearing somite, P5-bearing somite with fifth thoracopod and genital double-somite, lateral; E, pseudopericymbium, anal somite and left caudal ramus, lateral; F, same, dorsal. [Incised hyaline frill of P5-bearing somite arrowed in A and D.]

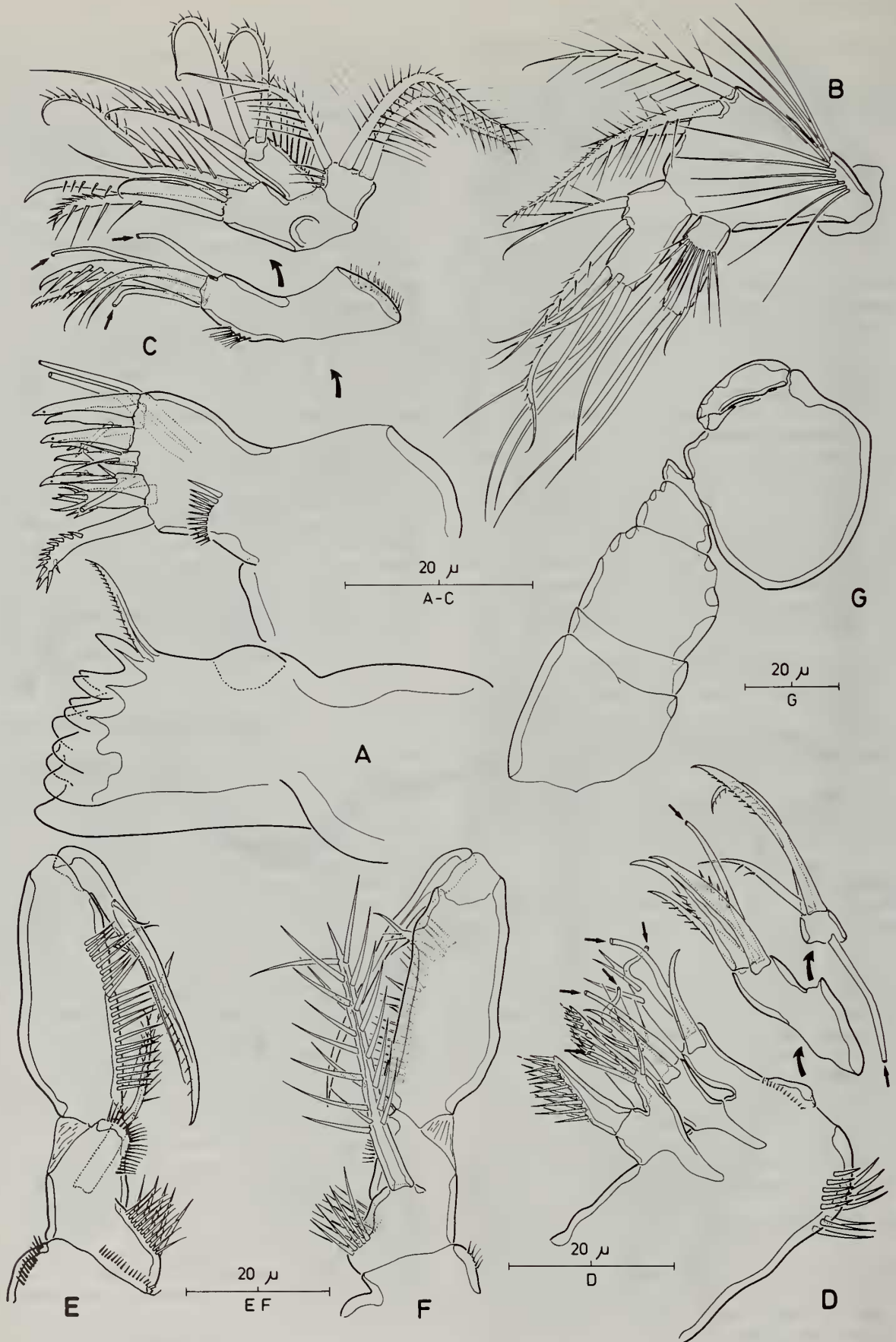


Fig. 15 *Danielssenia typica*. A, Mandible, gnathobase; B, mandible, palp; C, maxillula, posterior, showing disarticulated praecoxa, coxa and palp; D, maxilla, showing disarticulated syncoxa, basis and endopod; E, maxilliped, anterior; F, maxilliped, posterior; G, male antennule (armature omitted). [Tubular setae arrowed in C-D.]

row of long setules at 1/3 distance from the proximal margin, and 1 lateral, 1 subapical and 2 apical setae.

Maxillule (Fig. 15C). Praecoxal arthrite with 9 spines and 1 tubular seta around the distal margin, and 2 geniculate tubular setae on the anterior surface; coxal endite with 1 pinnate spine, 1 setulose claw, 1 smooth setae and 3 tubular setae; basal endites closely set, proximal with 2 setae, distal with 2 setae and 2 spines; rami with 3 setae each.

Maxilla (Fig. 15D). Praecoxal endite with 2 unilaterally pinnate spines and 1 basally fused spine bearing tubular extension. Coxal endites with 1 spine and 2 tubular setae each. Allobasis with 2 articulating claws, 1 pinnate spine and 1 tubular seta. Endopod with 1 tubular seta, 1 spine and 2 pinnate setae.

Maxilliped (Figs 15E-F). Syncoxa with 1 large setulose spine posteriorly and 1 smaller pinnate seta anteriorly. Basis with anterior row of long spinules and small, pinnate seta on palmar margin. Endopodal claw with 2 accessory setae.

Intercoxal sclerites of P2-P4 (Fig. 16H) not U-shaped and provided with large spinules on anterior surface (as in *Archisenia*).

P2 endopod of male (Figs 16A-B). Inner setae of proximal and middle segments reduced compared to the female. Outer apophysis of middle segment very large, reaching far beyond the distal segment. Inner setae of distal segment spiniform and stouter than in the female; inner terminal seta reduced, with spatulate tip; outer terminal seta represented by small setule; outer spine curved at tip and standing on cylindrical process.

P3 endopod of male (Fig. 16C) with acutely recurved process anteriorly at outer distal corner of middle segment.

Genital field with minute copulatory pore (Fig. 16D) leading via short sclerotized duct to multi-chambered seminal receptacle (Figs 16F-G). Copulatory duct entering unpaired ventral chamber leading dorsally to paired reservoirs both anteriorly and posteriorly. Anterior reservoirs largest and extending to posterior part of P5-bearing somite (Fig. 16D). P6 in female represented by 1 plumose seta and 2 minute spiniform elements (Fig. 16E). P6 of male with 1 plumose and 1 pinnate seta (Fig. 16J).

REMARK. Shen & Bai (1956) pointed out that either 1 or 2 setae can be found on the middle endopod segment of P2, however, their figured specimen with 2 setae on this segment (Plate XI, Fig. 86) is almost certainly an aberrant case. The same applies to the armature of the baseoendopod of the male specimens reported on by Gee (1988b) where a 'variable' number of setae can be found; all setation patterns diverging from the typical bisetose condition are aberrations caused by abnormal copepodid development.

(v) Amended diagnosis

As a result of the arguments put forward above, the genus *Danielssenia* now contains only 3 well defined species and we have re-diagnosed the genus accordingly:

Paranannopidae. Body variable in size, slightly fusiform and dorso-ventrally flattened. Rostrum hyaline, large, typically deflexed, with 2 pairs of small sensillae. Somatic hyaline frills minutely dentate except for deeply incised frill on dorsal margin of P5-bearing somite. Original segmentation of female genital-double somite marked by complete subcuticular ridge; genital field with small copulatory pore; short copulatory duct leading to seminal receptacle with paired,

anteriorly directed chambers extending to anterior margin of genital double-somite; P6 with 1 outer plumose seta and 2 minute spiniform elements. Pseudoperculum hyaline with deeply incised margin. Caudal rami parallel, broader than long, seta I minute. Female antennule 4-segmented; aesthetasc on segment 3; terminal segment with strong pinnate spines. Antennary exopod 3-segmented with armature formula [1-1-3]. Mandibular coxa with blunt teeth and 1 seta on gnathobase, basis broad with 3 setae on distal margin; endopod 1-segmented; exopod 1-segmented, with 1 lateral and 3 distal setae. Maxillule with 3 tubular setae, 1 pinnate seta and 1 spine on coxal endite; basal endite with 4 setae and 1 spine. Maxilla with tubular setae on coxal endites, allobasis and endopod; praecoxal endite with 3 pinnate spines. Maxilliped subchelate with 1 large and 1 small seta on syncoxa; basis with small pinnate seta on palmar margin, endopodal claw with 2 accessory setae. P1 exopod 3-segmented, exp-3 with distal outer spine longer than middle outer spine; endopod 2-segmented, enp-2 4 times longer than broad, inner seta implanted medially. P2-P4 intercoxal sclerites with spinules on distal margin; rami 3-segmented; exp-1 without inner seta. Armature formula of P1-P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	0.1.(1-2)23	1.1.221
P3	0.1.(1-2)23	1.1.(1-2)21
P4	0.1.(2-3)23	1.1.(0-1)21

Female fifth pair of legs not fused medially; exopod and baseoendopod separate, each with 4 or 5 setae.

Male with sexual dimorphism on antennule, P2 endopod, P3 endopod, P5, P6, and in genital segmentation. Antennule 8- to 9-segmented, subchirocer; segment 6 very swollen, with aesthetasc. P2 enp-2 with inner seta, outer distal corner attenuated into a long apophysis reaching far beyond the distal border of enp-3; enp-3 with distal outer spine and 2 terminal setae very reduced, inner setae spiniform and larger than in female. P3 enp-2 with outer distal corner attenuated into a recurved apophysis. P5 of each side fused medially; baseoendopod and exopod separate with 2 and 4 or 5 setae, respectively. P6 symmetrical, fused to somite, with 2 setae each.

TYPE SPECIES. *D. typica* Boeck, 1872 (by monotypy). [syn.: *D. fusiformis* (Brady, 1880) sensu Sars (1910)].

OTHER SPECIES. *D. quadriseta* Gee, 1988; *D. reducta* Gee, 1988.

SPECIES INQUIRENDA. *D. similis* Chislenko, 1971.

Key to species

1. P2-P3 exp-3 with 2 inner setae, P4 enp-3 with 1 inner seta ... 2. P2-P3 exp-3 with 1 inner seta, P4 enp-3 without inner seta *D. reducta* Gee, 1988.
2. P3 enp-3 with 2 inner setae, P5 exopod with 5 setae in both sexes *D. typica* Boeck, 1872. P3 enp-3 with 1 inner seta, P5 exopod with 4 setae in both sexes *D. quadriseta* Gee, 1988.

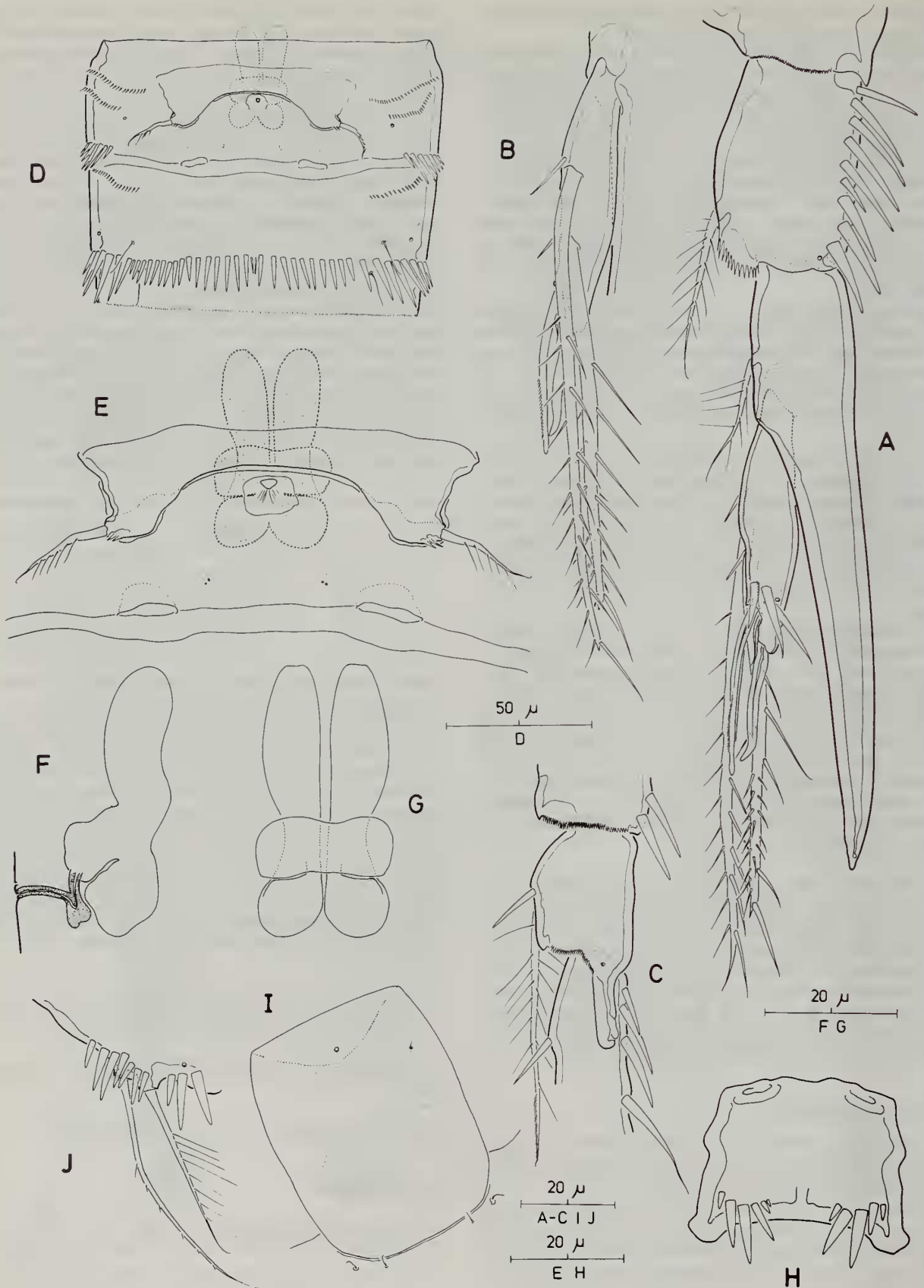


Fig. 16 *Danielssenia typica*. Male: A, P2 endopod, anterior; B, distal segment of P2 endopod, posterior; C, P3 endopod, middle segment, anterior; H, intercoxal sclerite P3; J, sixth leg. Female: D, genital double-somite, ventral; E, genital slit and copulatory pore; F, seminal receptacle, lateral; G, same, ventral; I, rostrum.

Genus *Bathypsammis* gen. nov.SYNONYMY. *Psammis* Sars, 1910 (part.).

DIAGNOSIS. Paranannopidae. Body large, more or less cylindrical. Rostrum not hyaline, with 2 pairs of sensillae, anterior pair large. Somatic hyaline frills minutely dentate. Female genital double-somite with lateral and ventral sub-cuticular ridge, marking original segmentation; copulatory pore minute; copulatory duct and seminal receptacle unconfirmed; P6 with 2 setae and 1 setule in between. Pseudoperculum hyaline, vestigial. Caudal rami divergent, elongate (length about 5 times proximal width); with tuft of long setules near inner distal corner; dorsal surface with chitinized rim in anterior half. Female antennule 4-segmented; aesthetasc on segment 3; distal 2 segments with heavily pectinate spines. Antennary exopod 3-segmented with armature formula [2-1-3]. Mandibular coxa elongate, gnathobase with blunt teeth and spinule row; basis broad with 4 setae on distal margin; endopod 1-segmented, slightly longer than exopod; exopod 1-segmented with 1 lateral and 2 apical setae. Maxillule without modified spines on coxal endite; basal endite with 5 setae. Maxilla without tubular setae; praecoxal endite with 3 pinnate spines (1 fused to endite). Maxilliped subchelate; armature of syncoxa unconfirmed; basis with naked seta on palmar margin, endopodal claw with 2 accessory setae. P1 with very long outer basal seta reaching to middle of exp-3; exopod 3-segmented, exp-3 with distal outer spine longer than middle outer spine; endopod shorter than exopod; 2-segmented, enp-2 as long as enp-1, inner seta implanted at 1/3 distance from proximal margin. P2-P4 intercoxal sclerites with few long setules; rami 3-segmented; exp-1 with inner seta; female P2-P3 enp-2 without apophysis at outer distal corner. Armature formula of P1-P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.223	1.2.121
P3	1.1.323	1.1.121
P4	1.1.323	1.1.121

Female fifth pair of legs not fused medially; exopod and baseopod fused to form a bilobate plate; exopodal lobe with 2 spines and 2 setae; endopodal lobe with 2 setae and 3 spines, the outer 2 of which are stubby.

Male unknown.

TYPE SPECIES. *Bathypsammis longifurca* (Bodin, 1968) comb. nov.

OTHER SPECIES. None.

ETYMOLOGY. The generic name is derived from the Greek *bathys*, meaning deep, and *Psammis*, probably the most closely related genus known in the Paranannopidae. Gender: feminine.

Bathypsammis longifurca (Bodin, 1968) comb. nov.

SYNONYMY. *Psammis longifurca* Bodin, 1968.

MATERIAL EXAMINED. From Dr Ph. Bodin; holotype dissected on 3 slides and now deposited in the collections of The Natural History Museum under reg. no. 1992.1091; Bay of

Biscay, Stn 308 (46°07' N; 05°00' W), depth 3950 m; coll. August 13 1963, R/V *Job-ha-Zelian*.

Bodin's (1968) excellent original description is supplemented here by the following observations and Figures 17-18.

Antennule 4-segmented, third segment homologous to segments 3-4 in *Archisenia*. Distal segment with large, swollen seta anteriorly near proximal corner; as pointed out by Bodin this segment is seemingly subdivided by the raised insertion site of one of the large pectinate spines (Fig. 18A). Armature formula: [1, 8, 14+ae, 16].

Mandibular gnathobase (Fig. 17B-C) with 4 long teeth, one trifold, slender element and 1 pinnate seta; a comb of spinules is present at the base of the smaller teeth. The endopod has 1 outer, 1 subapical and 6 apical setae (2 of which are fused basally).

Maxillule (Fig. 17D). Praecoxal arthrite with 9 spines and 1 tubular seta around the inner margin, and 2 geniculate tubular setae on the anterior surface; coxal endite with 4 setae, pinnate spine and straight spine with defined flexure zone and small pore near the apex; basal endite with 5 setae.

Maxilla (Fig. 18B-C) with praecoxal endite drawn out into heavily pectinate spine and bearing 2 articulating elements; coxal endites with 1 serrate spine and 2 setae each. Allobasis with 1 short and 2 long setae; endopod with 4 setae.

Maxilliped (Fig. 18D). Syncoxa missing in preparation. Basis with naked seta on inner margin, 2 spinular rows on anterior surface and another one on posterior surface; endopodal claw with 2 accessory setae.

Intercoxal sclerites of P2-P4 U-shaped (as in *Fladenia*) and provided with few long setules near lateral margins.

Fifth leg (Fig. 17E) with 2 large tube pores on anterior surface.

Genital field (Fig. 18E) with minute copulatory pore. The internal structures of the genital double-somite were destroyed during the dissection, so no observations of the copulatory duct and the seminal receptacles could be made.

Pseudoperculum very weakly developed. Distribution of caudal rami setae as in Fig. 18F-G; seta III dislodged in both rami, insertion site indicated by small socle (Fig. 18G).

P. longifurca does have certain features in common with *P. longisetosa* and *P. longipes*, namely: anterior pair of rostral sensillae enlarged (Fig. 17A); only 1 lateral seta on both rami of the mandible (Fig. 17B); 2 setae on exp-1 of the antenna; 2 setae on enp-2 of the P2; and fused rami in the female P5. However, *P. longifurca* lacks certain important features shared by the other two species, namely: no large strongly pinnate seta on the basis of the maxilliped, the seta on this segment being small and naked (Fig. 18D); the endopod of P2 is not distinctly longer than the exopod; the proximal inner seta of P2 enp-2 is not displaced to the posterior surface; the inner distal seta of P3-P4 enp-3 is not reduced; and, there is no attenuation of the outer distal corner of P2 enp-1. Finally, *P. longifurca* has a number of characters which are not shared by the other members of this genus such as: (i) a plume of long fine setules at the inner distal corner of the caudal ramus; (ii) an outer basal seta on P1 which is nearly as long as the exopod; (iii) a P1 endopod which is shorter than the exopod and in which both segments are equal in length; (iv) a P5 with peculiar spines on the endopodal lobe and a minute outer basal seta; (v) a primitive setal formula for the exopods of the swimming legs which is shared only by *Archisenia* and *Jonesiella*. On the basis of these characters we assign *P.*



Fig. 17 *Bathysammis longifurca* comb. nov. Female: A, rostrum; B, mandible; C, mandible, gnathobase; D, maxillule, praecoxa disarticulated; E, P5, anterior.

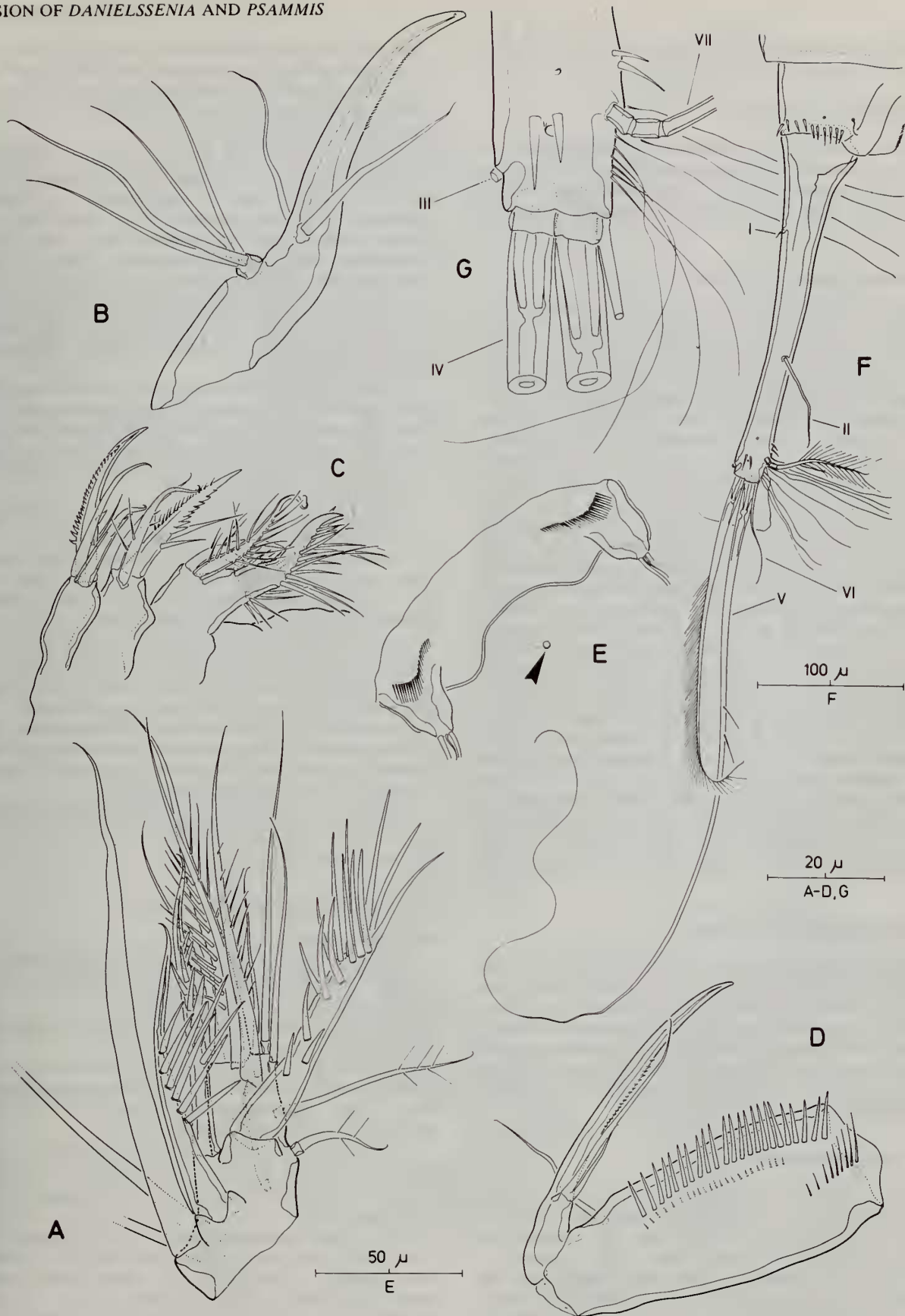


fig. 18 *Bathypsammis longifurca* comb. nov. Female: A, antennule, distal segment; B, maxilla, allobasis and endopod; C, maxilla, syncoxal endites; D, maxilliped, anterior (syncoxa missing); E, genital apertures and copulatory pore (arrowed); F, anal somite and left caudal ramus, dorsal; G, caudal ramus, detail of posterior margin.

longifurca to a new genus *Bathypsammis* which is closely related to *Psammis*.

Genus *Psammis* Sars, 1910

With the removal of *P. longifurca* to *Bathypsammis* gen. nov., the number of species currently allocated to the genus *Psammis* is reduced to four: *P. longisetosa* Sars, 1910; *P. borealis* Klie, 1939; *P. kliei* Smirnov, 1946; and, *P. longipes* Becker, 1974.

(i) *Psammis borealis* Klie, 1939

This species was first briefly diagnosed in 1939 from material collected in deep water near Iceland. A more extensive description, accompanied by illustrations, was published in 1941. Any justification for placing this species in *Psammis* is missing from Klie's (1939, 1941) papers, providing instead a large number of fundamental differences with the type species *P. longisetosa*. We have re-examined Klie's type material of *P. borealis* (Cop. 211–215; 4 ♀♀, 1 ♂, all dissected on slides; Zoologisches Museum der Universität Kiel). The slide of the male is somewhat confusing in that there seems to be 3 mounted antennules which do not show male characteristics and only part of one which does have the features of a male. Further, the limbs on this slide show no sexual dimorphism on either P2 or P3. The genital somite is also missing and the only appendage that differs from the slides of the females is the P5. The fifth legs of both sexes are exactly as drawn in Figs. 4 & 6 in Klie (1941). However, based on the mouthparts and the setation of the female thoracopods, and pending more information on swimming leg sexual dimorphism, we propose to retain this species within the Paranannopidae as *species incertae sedis*. It should be noted here that the specimens labelled *P. borealis* and deposited in the Smithsonian Institution (reg. no. 00231018) by Prof. Dr B.C. Coull are not the same genus as that of Klie (1939). This material (2 ♀♀) collected from the North Carolina continental shelf [this record is not listed in Coull (1971)] closely resembles *Pseudotachidius similis* T. Scott, 1902 and *P. minutus* Itô, 1983.

(ii) *Psammis kliei* Smirnov, 1946

We have been unable to discover the type material of *P. kliei* described by Smirnov (1946) from Henrietta Island (New Siberian Islands, East Siberian Sea). However, the recent recovery of a specimen from Spitsbergen which we believe is referable to this species, indicates that it should be placed in another genus close to *Psammis* and *Danielssenia*. This will be discussed further in a future paper on the Paranannopidae of Spitsbergen (Gee & Huys, in prep.).

(iii) *Psammis longipes* Becker, 1974

MATERIAL EXAMINED. Holotype ♀ dissected on 2 slides (Becker collection; Zoologisches Museum der Universität Kiel, reg. no. 1009–1010); Peru Trough, R/V *Anton Bruun* Sta. 179, 12°03'S 78°45'W, depth 5000 m, leg. W. Noodt.

This species is known from the type locality only. The following redescription (Figs. 19–20) is confined to structures that were misinterpreted or not well illustrated in Becker's (1974) original description:

Mandible (Figs. 19A–B). Gnathobase with multicuspidate, elongate teeth decreasing in size dorsally, and with 2 pinnate

setae near the distal dorsal corner; coxa with large spinules around the base of the palp. Basis with 3 setae, middle one with shorter spinules. Endopod only slightly longer than exopod, with 1 lateral and 3 apical setae; exopod with 1 lateral and 2 apical setae.

Maxillule (Fig. 19C–D). Praecoxal arthrite with 9 pinnate spines and 1 tubular seta around the distal margin and with 2 geniculate tubular setae on the anterior surface. Coxal endite specialized; armature consisting of 3 tubular setae and 3 spines; largest (= anterior) spine with broad base, a comb of flat spinules along the inner margin and ending in a tubular extension; middle spine also swollen at base and with fan of non-articulating flat spinules arranged around the apex; posterior spine with large spinule. Basal endite with 3 plumose setae and 1 short spine with tubular extension. Endopod and exopod with 3 setae each.

Maxilla (Fig. 19E). Praecoxal endite with 2 pinnate spines, distal one with tubular extension. Coxal endites with 2 spines and 1 seta each, distal spine and posterior seta with tubular extension. Allobasis with 2 articulating claws and a tubular seta on either anterior and posterior surface. Endopod with 1 simple and 3 tubular setae.

Maxilliped (Fig. 19F) as described by Becker (1974) except that the endopodal claw bears an accessory seta.

The armature formula given by Becker for the swimming legs is erroneous on two points: P3 enp-2 has only 1 inner seta, the proximal one shown in his figure being an enlarged spinule; P3–P4 exp-3 have an extra element distally, representing the reduced inner terminal seta (Fig. 20A–B).

Fifth leg (Fig. 20C). An incomplete furrow on the posterior surface marks the original proximal margin of the endopodal lobe. The 3 distal setae of this lobe are multipinnate.

Genital field (Fig. 20D) with small copulatory pore leading via linear duct to bilobate seminal receptacle largely located anterior to genital slit. P6 armature represented by pinnate seta and 2 minute spinules (vestigial setae?).

Hyaline frill of all body somites finely dentate; pseudopericulum well developed (Fig. 20E). Pattern of caudal ramus setae as in Fig. 20E.

(iv) *Psammis longisetosa* Sars, 1910

MATERIAL EXAMINED.

— Zoologisk Museum, Oslo: (a) G.O. Sars collection: F20223: 1 ♀ (in alcohol) and 1 ♂ (dissected); collected from Farsund (type locality), Norway; F20224: vial containing 19 ♀♀ and 6 ♂♂; collected from Risør, Norway;

(b) F20929: 4 ♀♀ (2 on slides, 2 in alcohol), 3 ♂♂ (1 on slide, 2 in alcohol); collected by J.A. Berg, deposited by J.M. Gee, from Bjørnehodebukta (59°42.8'N, 10°32.2'E), Oslofjord, 35 m depth, June 1984;

— The Natural History Museum: 1992.1096: 1 ♂ (in alcohol), 1 ♀ (on 6 slides), 1 ♂ prosome (on 7 slides); collected by R. Huys, from Frierfjord-Langesundfjord, 55 m depth, spring 1985.

The original descriptions of *P. longisetosa* given by Sars (1910, 1921) have been supplemented since by a complete redescription by Gee (1988a). The single female collected from Raunefjorden and figured by Por (1965) in all probability does not belong to *P. longisetosa*. In addition to the differences in the shape and armature of the P5 mentioned by Por, substantial discrepancies appear from his illustrations of the P1 (relative proportions of endopodal segments), last



g. 19 *Psammis longipes*. Female: A, mandible, posterior; B, mandible, gnathobase, anterior; C, maxillule, posterior; D, maxillule, detail of coxal endite; E, maxilla, posterior (showing syncoxal spines enlarged); F, maxilliped, posterior. [Tubular setae arrowed in C-E.]

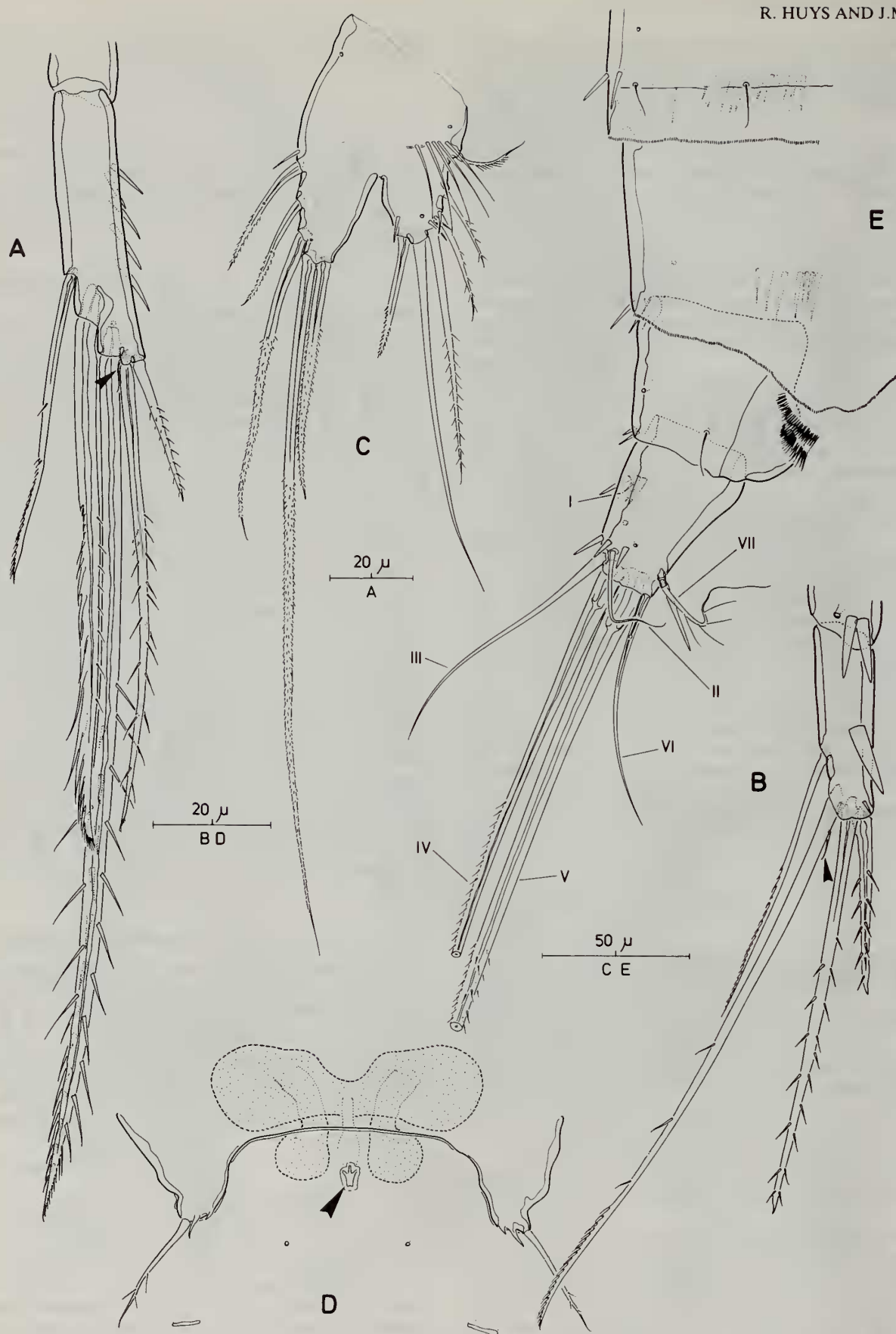


Fig. 20 *Psammis longipes*. Female: A, P3 endopod, distal segment; B, P4 endopod, distal segment; C, P5, anterior; D, genital apertures and copulatory pore (arrowed); E, posterior abdominal somites and left caudal ramus, dorsal. [Vestigial seta arrowed in A–B].

abdominal somites (ornamentation) and caudal rami (shape).

Re-examination of *P. longisetosa* has revealed a number of features that were overlooked or misinterpreted in earlier descriptions. In many cases these observations have shown an astonishing similarity in the detailed structure of the cephalic appendages between *P. longipes* and the type species.

The rostrum is not hyaline (Fig. 22A); the anterior pair of sensillae is enlarged. In the male the antennule is 9-segmented (Fig. 22A) and the segmental pattern is homologous to that of *Archisenia*.

Mandible (Fig. 21A–B). The gnathobase has similar multicuspidate teeth and 2 pinnate setae. The basis has 4 setae; the ornamentation of these setae shows that it is either the proximalmost or following seta that is missing in *P. longipes*. Both species have the same armature on the rami.

Labrum (Fig. 22B) with 1 large, median and a pair of smaller secretory pores on the anterior surface, and long spinules around the distal margin.

The detailed structure of the maxillule and maxilla is exactly the same as in *P. longipes*, including the presence and position of tubular setae and the modifications of the maxillary coxal endite.

The maxillipedal syncoxa has been invariably described as possessing a single, very large, spinulose seta, corresponding to the posterior seta in *P. longipes*; the smaller, setulose, anterior seta in this species is further reduced to a minute, pinnate spine in *P. longisetosa* (arrowed in Fig. 21C) and approaches the length of the largest ornamental spinules, the reason why it had been overlooked in previous descriptions.

The sexual dimorphism on the P2 endopod includes modifications of the middle and distal segments (Figs 21D–E). The anterior, spinous apophysis on the outer margin of the proximal segment is not a sexually dimorphic feature since it is also found in female specimens. The middle segment is drawn out into a large apophysis not reaching to the end of the distal segment and provided with an anterior secretory pore near the apex; the inner margin has 2 distally serrate setae, the proximal one being slightly displaced to the posterior surface; these setae are distinctly longer in the female. The distal segment possesses 4 articulating armature elements corresponding to the 2 inner and 2 terminal setae in the female; the outer spine in the female is modified in the male and replaced by a short, spinous process distally.

As in *P. longipes*, the reduced inner terminal seta of P3–P4 enp-3, represented by a setule, has been overlooked thus far (arrowed in Figs 21F–G). In the male the outer distal corner of the P3 middle segment is transformed into an acutely recurved process (Fig. 21F); the inner seta on this segment is distinctly longer in the female.

The fifth legs of both sexes are as in Figs 22E and F, respectively.

The original segmentation of the female genital double-somite is marked by a transverse chitinous rib dorsally and ventrally (Fig. 22D). The seminal receptacle is relatively small (Fig. 22C); the P6 is represented by 1 plumose seta and 1 small spinule in the female; in the male the sixth legs are fused and symmetrical, and bear 2 naked setae on either side (Fig. 22G).

(v) Amended diagnosis

Only *P. longisetosa* and *P. longipes* are retained in the genus *Psammis*, which is here redefined.

DIAGNOSIS. Paranannopidae. Body large, slightly fusiform and dorso-ventrally flattened. Rostrum not hyaline, with 2 pairs of sensillae, anterior one large. Somatic hyaline frills minutely dentate. Female genital double-somite with lateral and ventral sub-cuticular ridge marking original segmentation; genital field with minute copulatory pore and linear duct leading to transverse seminal receptacle located anterior to genital slit; P6 with 1 plumose seta and 1–2 minute spinulose elements. Pseudopericulum hyaline with dentate margin. Caudal rami divergent and longer than broad, tapering slightly. Female antennule 4-segmented; aesthetasc on segment 3; all segments with pinnate setae and spines. Antennary exopod 3-segmented with armature formula [2–1–3]. Mandibular coxa elongate, with finely pointed teeth and 2 setae on gnathobase; basis broad with 3–4 setae on distal margin; endopod 1-segmented, equal in length to exopod, with strongly reduced armature; exopod 1-segmented, with 1 lateral and 2 distal setae. Maxillule with 2 large comb-like spines and 3 tubular setae on coxal endite; basal endite with 3 plumose setae, 1 spine and 1 tubular seta. Maxilla with tubular setae on coxal endites, allobasis and endopod; praecoxal endite with 2 pinnate spines. Maxilliped subchelate with 1 large and 1 small seta (both pinnate) on syncoxa; basis with long plumose seta on palmar margin, endopodal claw with 1 accessory seta. P1 exopod 3-segmented, exp-3 with distal outer spine longer than middle outer spine; endopod at least as long as exopod, 2-segmented, enp-2 longer than enp-1, inner seta implanted medially. P2–P4 intercoxal sclerites without ornamentation; rami 3-segmented; exp-1 with an inner seta. P2 endopod distinctly longer than exopod; enp-1 with outer distal margin attenuated in both sexes; enp-2 with 1 inner margin seta and 1 seta implanted on posterior surface. Inner distal seta enp-3 P3–P4 extremely reduced and represented by setule. Armature formula of P1–P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.123	1.2.221
P3	1.1.223	1.1.321
P4	1.1.223	1.1.221

Female fifth pair of legs not fused medially; exopod and baseendopod fused to form a bilobate plate; exopodal lobe with 4–5 setae, endopodal lobe with 5 setae.

Male with sexual dimorphism in antennule, P2 endopod, P3 endopod, P5, P6 and in genital segmentation. Antennule 9-segmented, subchirocer; segment 6 swollen, with aesthetasc. P2 enp-2 with long outer apophysis not reaching to distal margin of enp-2; enp-3 with outer spine transformed into non-articulating process, distal setae reduced and inner setae enlarged compared to the female. P3 enp-2 with outer distal corner attenuated into a recurved apophysis. Fifth pair of legs not fused medially; endopodal lobe with 2 spines, exopod with 4 setae/spines. Sixth legs symmetrical, fused to somite, with 2 setae each.

TYPE SPECIES. *P. longisetosa* Sars, 1910 (by monotypy).

OTHER SPECIES. *P. longipes* Becker, 1974.

Ge (1988a) concurred with Wells' (1967) opinion that a generic distinction between *Danielssenia* and *Psammis* on the base of P5 segmentation alone can hardly be justified.



Fig. 21 *Psammis longisetosa*. Female: A, mandible, gnathobase; B, mandible, palp; C, maxilliped, anterior (small seta on syncoxa arrowed). Male: D, P2 endopod, anterior; E, P2 endopod, middle and distal segments, posterior; F, P3 endopod (small seta arrowed); G, P4 endopod (small seta arrowed).

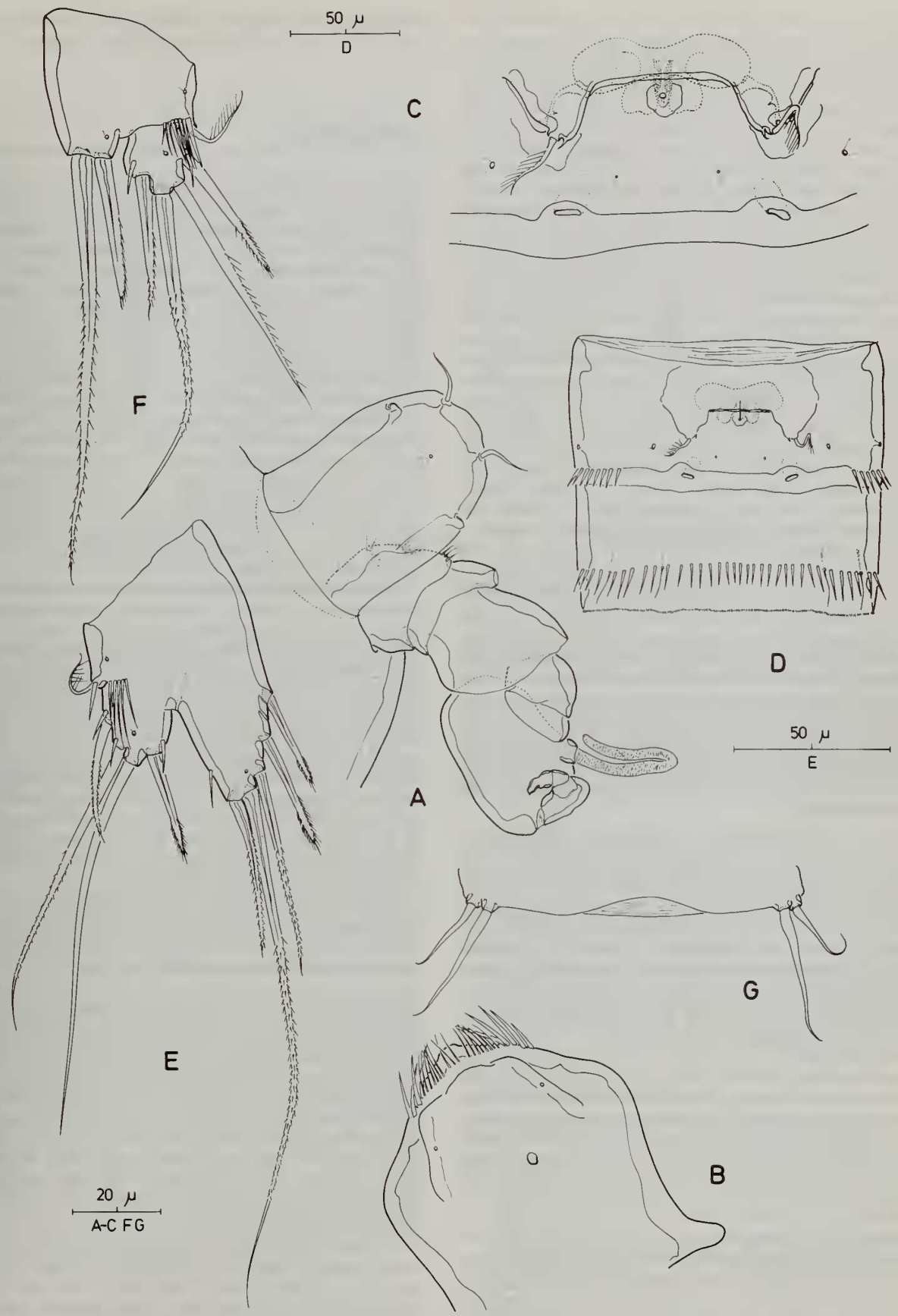


Fig. 22 *Psammis longisetosa*. Male: A, antennule and rostrum (armature omitted); F, P5, anterior; G, P6. Female: B, labrum, anterior; C, genital apertures and copulatory pore; D, genital double-somite, ventral; E, P5, anterior.

However, Gee also pointed out that the mandibular gnathobase in all *Psammis* species bears long, relatively fine, sharply pointed and widely separated teeth compared to the species of *Danielssenia* where these teeth are short, stout, blunt and closely set. On the base of this difference he suggested that both genera probably utilize different food items and to a certain extent are trophically isolated. In combination with the fused rami in the female P5, this evidence was considered as sufficient to maintain *Psammis*' separate generic status. Close examination of the mouthparts in *P. longisetosa* and *P. longipes* and comparison with *D. typica* has now revealed several other characters that can be used to distinguish both genera. Unique features for *Psammis* are the specialized comb-like spines on the coxal endite of the maxillule, the presence of only two spines on the praecoxal endite of the maxilla, and the extremely enlarged, spinulose seta on the maxillipedal basis. The presence of tubular setae and modified spines with tubular extensions on the maxillule and maxilla is a character that is shared by both genera though the precise number is not identical. It is conceivable that these specialized structures might perform a sensory role (as chemo- or probably mechanoreceptors) in remote food detection and/or manipulation. Both genera are predominantly found in the upper flocculent layer of muddy substrates where selection of food-particles probably requires a different mechanism. This could be particularly true for deepwater bottoms (fjords, abyss) where either turbidity is high or the proportion of suspended food-particles might fall below a subsistence level. The unique specialization of the mandibles, maxillules and maxillae might be viewed collectively as the result of a different dietary discrimination mechanism based on successful remote selection of food particles and thus avoiding the unnecessary high energy costs of rejecting unsuitable items upon initial capture. It is noted here that the claviform aesthetascs found on the mouthparts of certain other Paranannopidae (Gee & Huys, 1991) are not homologous to the tubular setae or modified spines bearing tubular extensions.

Another unique apomorphy of *Psammis* is illustrated by the setation pattern on the endopods of P3 and P4 (Fig. 23). The ancestral condition of P3 enp-3 is shown by e.g. *Archisenia* and consists of 1 outer spine (a), 2 distal spines (b-c) and 3 inner setae (d-f). This full complement of armature elements is also found in *Psammis* but is obscured by modifications in the distal part of the segment. The extreme reduction of the inner terminal spine (c) and the distad displacement of the distal inner seta (d) are the main reasons why the setal formula was erroneously cited as 221 (or 121 in P4) in previous descriptions. The distal elements expressed in this formula are b and d, rather than b and c. The spiniform and pinnate nature of seta d in *Psammis* did certainly contribute to this misunderstanding. The reduced condition in *Bathypsammis* (Fig. 23) has not evolved from the *Psammis* pattern but resulted through the loss of 2 inner setae. It is impossible to determine which seta (d, e or f) has been retained in *B. longifurca*.

Both species of *Psammis* can be differentiated by the number of setae on the mandibular basis (3 in *longipes*, 4 in *longisetosa*), the length of the anterior seta on the syncoxa which is distinctly longer in *P. longipes*, the ratio of endopod length to exopod length in P1 to P3 being much higher in *P. longipes*, the number of setae on the ♀ P5 exopod (4 in

longisetosa, 5 in *longipes*), and the gross difference in body size ($\pm 550 \mu\text{m}$ in *longisetosa*, $\pm 900 \mu\text{m}$ in *longipes*).

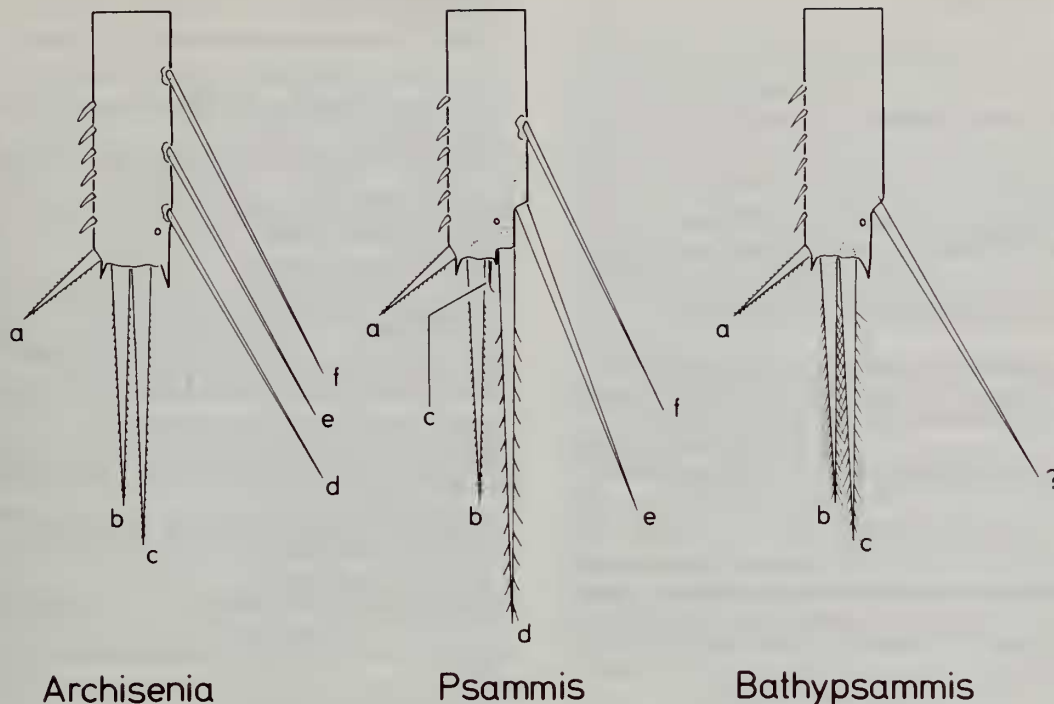
DISCUSSION

Within the Paranannopidae, aesthetascs on the mouthparts are a powerful synapomorphy for separating a number of genera which have recently been created or redefined, viz. *Jonesiella* (cf. Huys & Gee, 1992), *Paradanielssenia*, *Micropsammis*, *Telopsammis* and *Leptotachidia* (cf. Gee & Huys, 1991), *Sentiropsis* and *Peltisenia* (Huys & Gee, in press). The absence of such sensory appendages in *Archisenia* excludes it from this lineage and allies it with the more primitive danielsseniid genera, namely *Fladenia*, *Danielssenia*, *Psammis* and *Bathypsammis*. However, the phylogenetic relationships amongst these more primitive danielsseniid genera are somewhat unclear at the moment particularly with respect to the position occupied by *Archisenia*. The problem is that this genus shows a mosaic of primitive plesiomorphic characters (6-segmented female antennule; setal formula of legs P2-P4 with 7.8.8 setae/spines on exp-3 and 5.6.5 setae on enp-3; P5 with 5 setae on baseoendopod and exopod), but at the same time a number of unique autapomorphies in the sexual dimorphism on P1 basis, P2 enp-1 and P3 enp-2.

Within this group of genera it is clear that *Fladenia* is the most primitive genus because it retains both vestiges of sexual dimorphism involving a difference in the number of elements (in this case setae) on the endopod of P3 and P4 (Gee & Huys, 1990) and a primitive setal formula particularly in the exopods of P3 and P4. It is also clear that *Danielssenia*, *Psammis* and *Bathypsammis* are linked by a 4-segmented female antennule, a reduced number of setae on P4 enp-3 and probably by having only 2 setae on the P6 in the male (though the latter character cannot be scored for *Bathypsammis* since the male is unknown). Since it has no vestige of P3 and P4 setal sexual dimorphism and does not show the apomorphies of the *Danielssenia* lineage, it is likely that *Archisenia* diverged from the main evolutionary line after *Fladenia* and probably before the *Danielssenia*-grouping.

Within the *Danielssenia*-*Psammis*-*Bathypsammis* lineage, *Danielssenia* is considered the most advanced genus on account of the loss of a seta on exp-1 of the antenna, the basis of the mandible, exp-1 of P2-P4 and enp-2 of P2. Unique apomorphies for this genus are the typically ventrally deflected rostrum, the blunt teeth on the mandibular gnathobase, and the dorsal, incised, hyaline frill on the P5-bearing somite. Another diagnostic character for *Danielssenia* is illustrated by the shape of the seminal receptacle. Multi-chambered receptacles have been described for a number of Paranannopidae such as *Leptotachidia*, *Telopsammis*, *Psammis* and *Paranannopus* (Gee & Huys, 1990, 1990) and might well be the ancestral state in this family. However, in none of these genera the paired anterior chambers are elongate, cylindrical reservoirs extending into the posterior part of the P5-bearing somite.

Analysis of the precise relationships within the *Danielssenia* grouping is hampered by the absence of male *Bathypsammis*. The specialized tubular structures on the endites of the maxillule and maxilla provides a robust synapomorphy to link *Danielssenia* and *Psammis*. A close relationship is also indicated by the armature of the female sixth legs bearing one



Archisenia

Psammis

Bathypsammis

Fig. 23 Comparison of armature on distal endopod segment of P3 in *Archisenia*, *Psammis* and *Bathypsammis*.

plumose seta and 2 inner, minute spiniform elements (compared to 2 setae and 1 setule in between in *Bathypsammis*), and by a detailed comparison of the distal transformations in the male P2 endopod. Potential synapomorphies grouping *Psammis* and *Bathypsammis* are: (i) rostrum with enlarged anterior sensillae; (ii) the mandibular exopod with only 1 lateral and 2 apical setae; (iii) the fusion of the exopod and baseoendopod in the female P5. Some species of *Danielsenia*, however, also show a reduction in the setation of the mandibular exopod (e.g. *D. typica*), and the fused P5 in *Bathypsammis* might have been evolved convergently, since, in other respects, it is very different from the condition in *Psammis*. The rostral character might also be a product of convergence since the enlargement of the anterior pair of sensillae has evolved independently in a number of other deepwater genera such as *Paranannopus* and *Cylindronannopus*.

Unique apomorphies for *Psammis* are: (i) reduction of the mandibular endopod (1 lateral, 3 apical setae); (ii) the specialized comb-like spines on the maxillary coxal endite; (iii) praecoxal endite of maxilla with only 2 spines; (iv) extreme development of the posterior seta on the maxillipedal basis; (v) elongation of P2 endopod, being longer than the exopod; (vi) the apophysis on P2 enp-1 in both sexes; (vii) reduction of the inner terminal seta on P3–P4 enp-3. In *Bathypsammis* the unique apomorphies are confined to the female as the male is unknown: (i) a very long outer basal seta on the basis of P1; (ii) a very long caudal ramus with a plume of setules on the inner distal corner; (iii) the form of the setae on the endopodal lobe of the female P5.

KEY TO GENERA OF PARANANNOPIDAE

REMARK. This key also includes *Psammis kliei* Smirnov, 1946, which will be placed in a genus by itself in a forthcoming paper (Gee & Huys, in prep.), and the genus *Carolinicola* Huys & Thistle, provisionally assigned to the Paranannopidae by Huys & Thistle (1989).

1. P4 endopod 3-segmented 4.
P4 endopod 2-segmented, 1-segmented or absent 2.
2. Antennary exopod 1-segmented
..... *Carolinicola* Huys & Thistle, 1989.
Antennary exopod 3-segmented 3.
3. Body short, robust; caudal rami setae IV and V long and spinulose; P5 well developed, covering entire width of thoracic somite
..... *Paranannopus* Lang, 1936.
Body slender, cylindrical to vermiform; caudal rami setae IV and V short and plumose; P5 a minute plate, located midventrally *Cylindronannopus* Coull, 1973.
4. P2–P4 exp-1 without inner seta 5.
P2–P4 exp-1 with inner seta 7.
5. Antennules without plumose or pinnate spines/
setae *Sentiropsis* Huys & Gee, 1993.
Antennules with plumose and/or pinnate spines/setae 6.
6. Caudal ramus with distinct cluster of long setules at the inner distal corner; P2 enp-2 with large apophysis in ♀ (and presumably in ♂ also) *Psammis kliei* Smirnov, 1946.
Caudal ramus without such cluster; P2 enp-2 with large apophysis in ♂ only *Danielsenia* Boeck, 1872.
7. P4 exp-3 with 8 setae/spines 8.
P4 exp-3 with at most 7 setae/spines 13.
8. P2 enp-2 with 2 inner setae 9.

- P2 enp-2 with 1 inner seta 10.
9. Caudal rami 5 times as long as maximum width; P1 endopod shorter than exopod; P5 ♀ with fused exopod and baseoendopod *Bathypsammis* gen. nov. Caudal rami broader than long; P1 endopod longer than exopod; P5 ♀ with separated exopod and baseoendopod *Jonesiella* Brady, 1880.
10. Body dorsoventrally flattened; caudal rami setae IV and V stubby and spiniform; P1 enp-1 1.5 times as long as enp-2 *Peltisenia* Huys & Gee, 1993. Body not dorsoventrally flattened; caudal rami setae IV and V long and setiform; P1 enp-1 at most as long as enp-2 11.
11. Antennule ♀ 4-segmented; club-shaped aesthetascs present on mandible (endopod), maxillule (basis) and maxilla (endopod); P2 enp-2 ♂ without distinct outer apophysis *Paradanielssenia* Soyer, 1970. Antennule ♀ 6-segmented; no club-shaped aesthetascs on mouthparts; P2 enp-2 ♂ with long outer apophysis 12.
12. Antennary exopod with 1 seta on proximal segment; P3 exp-3 with 7 setae/spines; P2 enp-3 with inner distal seta transformed into large pinnate spine reaching beyond apophysis of enp-2 *Afrosenia* Huys & Gee, 1993. Antennary exopod with 2 setae on proximal segment; P3 exp-3 with 8 setae/spines; P2 enp-3 ♂ with inner distal seta not transformed and shorter than apophysis of enp-2 *Archisenia* gen. nov.
13. P2 enp-2 with 2 inner setae *Psammis* Sars, 1910. P2 enp-1 with 0–1 inner setae 14.
14. Club-shaped aesthetascs present on mandible (endopod), maxillule (basis) and maxilla (endopod); P2 exp-3 with at most 6 setae/spines 15. No club-shaped aesthetascs present on these appendages; P2 exp-3 with 7 setae/spines *Fladenia* Gee & Huys, 1990.
15. P1 enp-2 with 2 terminal setae geniculate; P5 ♀ baseoendopod and exopod indistinguishable, with 5 setae; P2 enp-2 ♂ without apophysis; P6 ♂ with 2 setae 16. P1 enp-2 with 1 terminal seta geniculate; P5 ♀ baseoendopodal and exopodal lobes indistinguishable, with 3 and 4 setae, respectively; P2 enp-2 ♂ with small apophysis; P6 ♂ with 3 setae *Micropsammis* Mielke, 1975.
16. Antennule in both sexes with densely opaque, bulbous appendage on distal segment P2–P4 exp-2 without inner seta *Leptotachidia* Becker, 1974. Antennule in both sexes without densely opaque, bulbous appendage on distal segment P2–P4 exp-2 with inner seta *Telopsammis* Gee & Huys, 1991.

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